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Long-term Qualitative Changes in Fish Populations and Aquatic Habitat in San Mateo Creek Lagoon, Northern San Diego County, California

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Abstract.—Patterns of abundance were documented for 17 species of fish in the lagoon at the mouth of San Mateo Creek, northern San Diego County, California from occasional observations (1974-1997) and multiple samples per year (1998-2008). Fish populations varied with Mediterranean climate patterns of rainfall, stream flow and consequent breaching of the lagoon to the ocean through the barrier sand berm. Two near-record rainfall seasons occurred during this period; the 1997-1998 El Niño due to southern storms and the 2004-2005 winter wet season of more usual storms from the north and northwest. The lagoon stabilized as fresh to brackish in the dry season and for multiple years during successive drier winters. Closed conditions benefitted the native, federally endangered southern tidewater goby, *Eucyclogobius kristinae*, but were less suitable for other native estuarine species more common in wetter years. Wet year flows also reduced non-native freshwater species; some thrived and increased predation pressure on the southern tidewater goby. Historically these exotics were absent and two additional native species were present, partially armored threespine stickleback, *Gasterosteus aculeatus*, and the federally endangered southern steelhead, *Oncorhynchus mykiss*. Restoring and maintaining a full suite of native species will require a combination of 1) habitat maintenance and restoration, 2) control or management of non-native species, and 3) reintroduction of some native fishes and amphibians.

Estuarine fish community studies exist for many California estuaries naturally or artificially open to the ocean on a year around basis (Allen et al. 2006). Most of these larger estuaries historically closed seasonally (Warme et al. 1977; Fong and Kennison 2010). Only a few studies exist for California systems still opening and closing in some approximation of the original Mediterranean climate-influenced hydrological cycles such as Ambrose and Meffert (1999) for Malibu Lagoon, Los Angeles County and Collins and Melak (2014) for Devereaux Slough, Santa Barbara County. Even then fish population composition and structure probably differ from the historical or original patterns (Lane 1977; Swift et al. 1989; USFWS 2005). Some native species have been extirpated from these systems and

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other non-native species have become established. San Mateo Creek Lagoon in coastal southern California and many smaller lagoons and estuaries still function in similar fashion to the original or historic hydrological patterns and provide insight to historical fish populations and their seasonal cycles. The addition of non-native species also provides insights to their interactions with, and effects on, the native fauna.

The number and composition of the native and non-native fishes fluctuates with the amount of freshwater inflow and degree of salt water invasion. These changes were documented to varying degrees from 1975 to 2008 in San Mateo Creek Lagoon in northern San Diego County, southern California and most intensively from 1996 to 2008. Collections were primarily to monitor the federally endangered southern tidewater goby, *Eucyclogobius kristinae* [then not separated from the northern species, *E. newberryi* (Swift et al. 2016)], and to remove invasive species. Other recent and historical records and observations added additional information. The objectives of this paper are to describe the fish community of San Mateo Lagoon and to document: 1) the seasonal and year-to-year fluctuations in abundance of the fishes (and a few associated aquatic organisms); 2) the interactions of native and non-native fishes; 3) assess the success of re-introduction of southern tidewater goby; and 4) provide management recommendations for restoration of the coastal lagoon habitat for native fishes.

Description of the Area

San Mateo Creek formed a small, narrow lagoon (wetted surface 1-4 ha) in northern San Diego County, California just south of the Orange County line (Fig. 1) and on the north edge of Marine Corps Base Camp Pendleton (MCB). It lies in San Onofre State Beach managed for recreation and habitat preservation by the San Onofre Unit of California State Park system. Emergent vegetation usually bordered the lagoon except for the sand berm at the mouth. After a few dry years even the berm became vegetated on the inland lagoon margin. Over 90% of the margin of the lagoon had tules (*Scirpus sp.*) or cattails (*Typha sp.*) with water cress or other emergent herbaceous plants near the shallower upper end. At higher water levels the lagoon invaded upstream into the riparian willow and cottonwood forest to or near the "Old Road Bridge" just downstream of the current Interstate 5 bridge (Fig. 1). As the lagoon warmed in the spring and water exceeded about 15° C in April or May, widgeon grass, *Ruppia*, and filamentous green algae began to regrow and filled much of the open water of the lagoon by fall. Some green algae floated, and onshore breezes pushed it inland to form spongy mats 2.5-7.5 cm thick covering the upper one-third to one-half of the lagoon by late summer or fall. Both the widgeon grass and green algae also were reduced in the fall and winter by cooler temperatures and grazing water fowl, mostly coots (*Fulica americana*). In the wet years some of these aquatic plants were scoured away by high flows.

In March 1998 strong El Niño storm flows and earth moving activities in the lagoon removed virtually all the marginal vegetation. The lagoon margin became partially revegetated as the season progressed and emergent aquatic vegetation gradually invaded into the lagoon over the next few years (Figs. 2-6). During the almost equally wet 2004-2005 winter season the rainfall and high stream flows were more evenly distributed, no excavation was performed, and marginal vegetation largely remained. The March 1998 El Niño flows also partially filled the lagoon with sediment reducing wetted area to 1-2 ha restricted to the seaward end of the lagoon (Fig. 2), extending 100-150 m upstream of the railroad bridge. Through subsequent years the lagoon enlarged to 3-4 ha when closed (Figs. 3-6)

Fig. 1. Aerial view of San Mateo Lagoon in typical summer/fall closed condition, separated from the ocean by a sand berm. Perennial creek originates in dry season from upwelling from the gravel at the right edge of the photo above the multilane Interstate 5 Freeway. The smaller two-lane "Old Road" bridge downstream is the earlier U. S. Hwy 1 Bridge dating from the 1930s. Figure by Edward Erwin, Brad Kelly, Merkel and Associates.

and extended 300 to 400 m above the railroad bridge. The water was up to 1.5 m deep at the lower end and gradually shallowed to the upper end. From 1998 to 2004 a deeper "hole" about 20 m in diameter and slightly more than 2 m deep was present about 100 m upstream of the railroad bridge on the north side.

Lagoon opening and closing was documented (Fig. 7) to varying degrees and was determined with direct observation and information from others working in the area. It strongly opened in early 1998 and early 2005 and 2006 and less in early 2000, 2001, and 2003. It was artificially opened to an unknown extent in January 2000 (State Parks Lifeguard, pers. comm.) and remained closed or opened only briefly in the other years. After initial opening due to high freshwater inflows along with scouring by longshore currents (Bascom 1980) the barrier sand berm rebuilt. The berm built progressively wider through the summer and fall reducing the likelihood of either ocean wave wash over or breaching and we did not observe or hear of any lagoon opening solely from surf action. At low tides low salinity water was observed seeping from the lower edges of the sand berm into the cobble habitat off the mouth of the lagoon. This seepage and evaporation was slightly higher than inflow since lagoon water level fell slowly through spring, summer, and fall as the sand barrier builds up higher and wider. In the second dry period after 2004-2005 the lagoon fell from 3-4 ha to less than 1 ha in wetted surface area by mid-2008.

Fig. 2. San Mateo Lagoon. Upper: Downstream view of lagoon from Old Road Bridge; Lower: Lagoon mouth from north. Lagoon partially open to the ocean. 11 June 1998.

Fig. 3. Upper: Downstream view of lagoon from Old Road Bridge; Lower: Lagoon mouth from north. Lagoon closing with vegetation beginning to encroach on lagoon. 14 July 1999.

Fig. 4. San Mateo Lagoon. Upper: Downstream view of lagoon from Old Road Bridge; Lower: Lagoon mouth from north. Increased vegetation and closed to the ocean. 29 June 2000.

Fig. 5. Upper: Downstream view of lagoon from Old Road Bridge; Lower: Lagoon mouth from north. Further vegetated and narrowly open. 30 March 2001.

Fig. 6. Upper: Downstream view of lagoon from Old Road Bridge; Lower: Lagoon mouth from north. Lagoon extensively vegetated and narrowly open to the ocean. 23 June 2003.

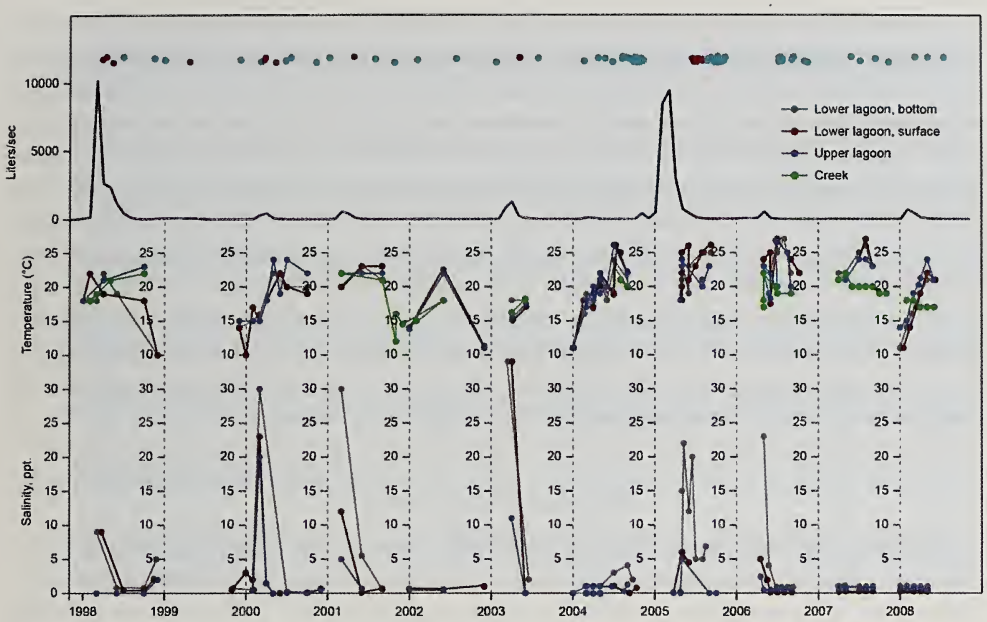

Fig. 7. Water temperature and salinity at San Mateo Creek and Lagoon, 1998-2008. See text for locations and methods of measurement. Dotted vertical lines represent January 1st of each year.

The substrate of the lagoon was over 90% sand. Some marginal pockets of finer clay or mud exist as well as scattered small stones or even gravel at the upper end near the stream mouth. After winter flows the sand was relatively unconsolidated. A 1-3 cm marl-like or flocculent layer intermixed with filamentous green algae developed over the sand as the warm season progressed. This layer persisted unless flushed out during high flow events. During summer and fall closures and winters when the lagoon failed to open, the salinity remained $\leq$ 3‰ with the deep pocket $\leq$ 5‰. When open and while closing again over days or weeks the lower lagoon became stratified with salinities up to 34‰ near the bottom in the lower one third or so of the lagoon (Fig. 7). In the spring of 2005 the saline bottom layer retained some ocean or sea water derived luminescence lacking in the upper, fresher layer. The water temperature ranged from 9-11° C in mid-winter and up to the mid-20s in midsummer in most of the lagoon. In the spring the surface of the lower lagoon and shallow upstream margins warmed faster than the bottom water but by summer and fall the temperature only varied one or two degrees between top and bottom. The inlet stream was close in temperature to the lagoon in the earlier years since it was also open to solar warming. In later years riparian canopy allowed the stream to remain cooler in summer, $\leq$ 21° C. Small areas of the upper lagoon under floating algal mats also remained cooler than the main lagoon as at times did the shaded areas under the ends of the railroad trestle. Dissolved oxygen (DO) and pH were taken less frequently than temperature and salinity; DO was almost always $\geq$ 4 mg/l and less a few times only at the bottom of the deeper area along the north shore about 100 m upstream of the railroad bridge. The pH was mostly between 6.4 and 9.6 except on 29 July 2004 when the values were between 4.4 and 5.9. Water was very turbid during storm flows, but the stabilized lagoon was usually clear with good visibility down to 1 m or more and became more cloudy and greenish in the warm months presumably due to the development of phytoplankton.

San Mateo Creek drains about 355 km^2 up to elevations of 1090 m largely on MCB and San Mateo Canyon Wilderness of the U. S. Forest Service in the Santa Margarita Mountains. It has no major impoundments or dams and few small residential or agricultural ponds on a few tributary canyons. Creek flow varied widely and was at or near record highs twice; the 1997-1998 El Niño year and the 2004-2005 rainfall year (Fig. 7, top). In contrast the years of 1998-1999, 2001-2002, and 2003-2004 were years of exceptionally low rainfall. The surface flow dried in the lower 7-8 km of creek except for a small perennial flow of 28-56 liters/sec into the upper lagoon, upwelling in the stream bottom about 150 m upstream of the northbound Interstate 5 bridge. In February 2002 up to 3785 l/day were added to the stream from dewatering related to construction on the Interstate 5 bridge. Sections of perennial flow existed in mountainous headwaters 8-15 km upstream (Hovey 2004; Swift, Holland, pers. obs.). The lower 7-8 km of alluvial valley absorbed the first winter rains and continuous surface flow took multiple storm events.

Materials and Methods

Sampling objectives were: 1) presence-absence surveys and monitoring of the federally endangered southern tidewater goby, *Eucyclogobius kristinae* (1991, 1993, 1996, 1998-2008); and, 2) removal of non-native predators considered threats to populations of the native fishes, amphibians and reptiles (1998-2000; 2004-2008). Sampling was conducted with seines 3.2 X 1.2 and 5 X 1.8 m with 3 mm square knotless mesh with 28.35 g weights every 15 cm, and 9.1 X 1.8 m, 9 mm square mesh similarly weighted. Non-native fishes, amphibians, and crayfish were also targeted with frog gigs (spears), Gee's minnow and crayfish traps, and larger fyke nets. More visits and seine hauls were taken in 1998-2003 to monitor presence/absence of tidewater goby, and in 2004 to 2008 to remove non-native fish (Appendix I), crayfish (*Procambarus clarki*), bullfrog (*Rana catesbeiana*) larvae (tadpoles) and non-native turtles. Fishes were identified and counted in the field, larger numbers ≥50 sometimes were estimated to avoid stressing native species. Native fish, amphibians, and reptiles were released at the site of capture and exotics were removed. Swift was present for virtually all sampling; voucher specimens were deposited in the Section of Fishes, Natural History Museum of Los Angeles County (LACM) and genetic vouchers of southern tidewater goby in the Jacobs Laboratory, University of California, Los Angeles. The catch data in the Appendix I are based on the seine hauls, 4 to 49 (average 24.2) per visit usually distributed over two thirds or more of lagoon. Length and width of seine hauls was recorded and catch-per-unit-effort (CPUE) was calculated by dividing the number of fish caught by total area seined. The mesh of the larger seines, 9 X 9 mm square (81 mm^2) was considered nine times more likely to allow small species to pass through than the smaller 3 X 3 mm square (9 mm^2) mesh. For calculation of CPUE for the two common small species, southern tidewater goby and mosquitofish, the catch data for larger mesh nets (Appendix I) were multiplied by nine for the graphs. The more frequent samples in 2004-2006 were grouped by month for calculation of CPUE. Hierarchical cluster analyses with complete linkage were performed for six scenarios, namely utilizing all species for the time period 1998-2008, and for two subsets, each including a strong wet year and the subsequent drier ones, 1998-2003 and 2004-2008. Three additional analyses utilized these same time periods with a subset of the 12 most common species. Water quality (temperature, salinity, pH, dissolved oxygen, and turbidity) was taken at the surface and bottom in water ≥ 1 m deep with an Horiba U-10 water quality instrument; in shallower water one sample was taken at mid-depth. Often only temperature and salinity were taken with a hand-held thermometer

and refractometer, respectively. These were taken in mid to late afternoon at three to six representative locations around the lagoon before seining mixed the water column. During periods of lagoon closure water quality data were taken intermittently since lagoon conditions changed very little over weeks or months. The lower lagoon data were in the deepest portion of the lagoon seaward of the railroad trestle and the upper lagoon varied from 100-150 to 350-400 m above the lagoon depending on water levels. Only water temperature was taken in the creek. Stream flow data for San Mateo Creek was from the USGS Web Interface for Gauging Station (USGS 11046300, San Mateo Creek near San Clemente), about 7 km upstream of the ocean. Fish sampling was done less frequently in the tributary creek above the lagoon but usually at least once in months sampling was done. On 26-27 November 2001 a stream diversion for bridge construction isolated 113 m of the creek centered on the Interstate 5 bridge and all native fish were removed and placed in the lagoon. On 8 February 2002 a similar effort was undertaken on 93 m of the previously established channel. The stream was 1-4 m wide, to 60 cm deep, with an estimated average depth of 10 cm, flow of $\leq$56 l/sec.

Results

The dates, number of seine hauls, areas seined, species, and catch numbers are presented in the Appendix I. Seine hauls captured 53,435 fishes among seventeen species and 92% of the fishes captured were southern tidewater goby (22,478; 42%) and mosquitofish, *Gambusia affinis* (26,966; 50%). Three other species were over 1%, namely black bullhead, *Ameiurus melas* (1096; 2.0%), deepbody anchovy, *Anchoa compressa* (922; 1.7%) and green sunfish, *Lepomis cyanellus* (796; 1.5%) and the remaining species under 1% each; striped mullet, *Mugil cephalus* (264), slough anchovy, *Anchoa delicatissima* (261), grunion, *Leuresthes tenuis* (246), staghorn sculpin, *Leptocottus armatus* (140), largemouth bass, *Micropterus salmoides* (122), topsmelt, *Atherinops affinis* (62), California killifish, *Fundulus parvipinnis* (51), arrow goby, *Clevelandia ios* (14), reef surfperch, *Micrometrus aurora* (8), yellowfin goby, *Acanthogobius flavimanus* (6), longjaw mudsucker, *Gillichthys mirabilis* (2), and bluegill, *Lepomis macrochirus* (1). On 11 April 2007 a small goldfish, *Carassius auratus*, about 3.8 cm was speared in the lagoon while searching for bullfrogs. After March 1998 high stream flows and earth-moving efforts to protect the railroad bridge southern tidewater goby were not detected for two years, presumed extirpated, and 520 were introduced from San Onofre Lagoon on 7 January 2000.

Number of species (richness) was highest during and within weeks to months of lagoon opening or breaching during wet years (Appendix I). The actual numbers of fish caught was lower during these periods and highest during intermediate low rainfall years when the lagoon did not open or only opened briefly, for a few days or weeks. During dry seasons or successive dry years in the fresh or nearly fresh lagoon populations of the two overwhelmingly dominant species, the native southern tidewater goby and non-native mosquitofish increased. These two species were almost continuously present except that the tidewater goby was extirpated twice during the study, and likely a third time historically in the early 1980s as discussed below. The goby was not detected on two occasions in early 2000 probably because of the small number introduced were likely decimated by the artificial opening of the lagoon noted above. They began to reproduce later and rose to large numbers later in 2000 reflecting an expanding population. A similar increase occurred in 2005 when high flows reduced the gobies and they increased later in the year.

The numbers of both native and non-native fishes usually increased during the warm months and usually declined in the cool months (Figs. 8 and 9). During wet years this

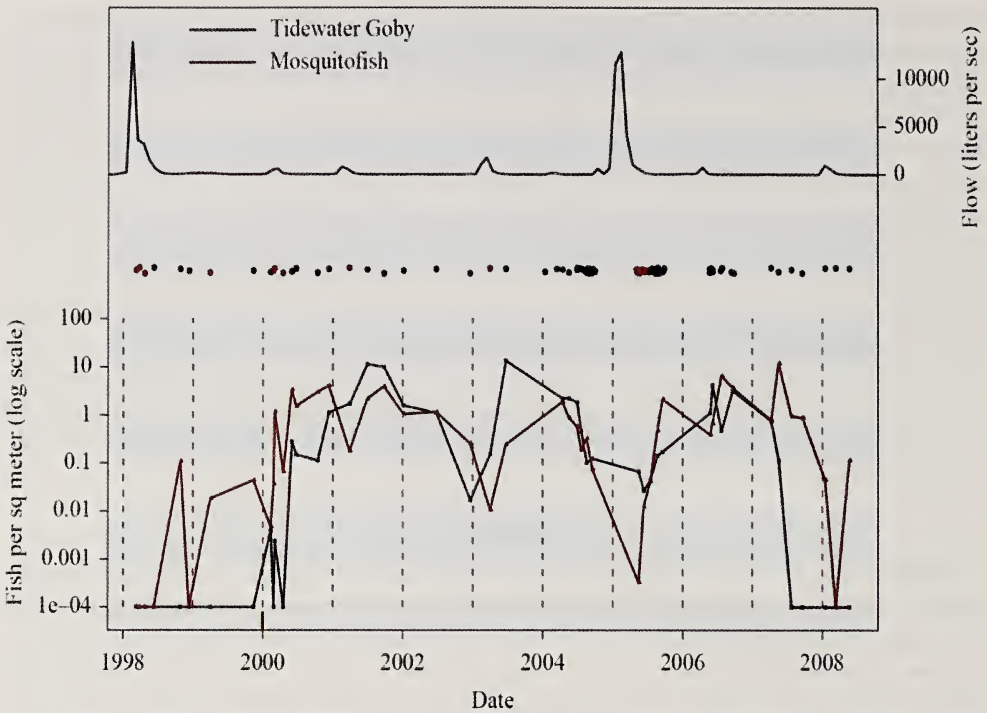

Fig. 8. Abundance of southern tidewater goby and mosquitofish, the two overwhelmingly common species in San Mateo Lagoon, 1998-2008. Catch data from Appendix I was multiplied by the indicated multiplier and plotted on a log scale. Dotted vertical lines represent January 1st of each year.

increase was partly due to reproduction by topsmelt and anchovies as well as Tidewater Gobies and Mosquitofish. During dry years when the lagoon remained fresh or brackish, the increase in southern tidewater gobies and mosquitofish was augmented by smaller increases in Green Sunfish and Black Bullhead, particularly after the 2004-2005 wet season.

The native estuarine fish species, topsmelt, slough anchovy, and deepbody anchovy came in as adults during the wet years and successfully spawned. Other native estuarine species entered during wet years as juveniles, survived and often were trapped if the lagoon remained closed, including California killifish, staghorn sculpin, arrow goby, longjaw mudsucker, and striped mullet. They were only rarely encountered as surviving adults under closed conditions. They reproduce in tidal estuaries or marine environments and only the California killifish reproduced in the lagoon based on about 10 small juveniles (10-20 m SL) taken on 23 June 2000 after the lagoon had been closed for at least a month. Otherwise California killifish were rare and usually only present during or soon after the lagoon had been open. Two adult California killifish recorded on 14 October 1993 in a long-closed lagoon were seen snorkeling and not taken in seine hauls. Twice in mid-May, 2005, eight reef surfperch, *Micrometrus aurora*, were taken in the lower lagoon during an open period and undoubtedly strayed from the rocky and cobble intertidal habitat off the mouth of the lagoon. Small juveniles of the non-native estuarine species, the yellowfin goby, *Acanthogobius flavimanus*, also were taken during some open lagoon periods (5) and one large adult was taken from the long-closed lagoon.

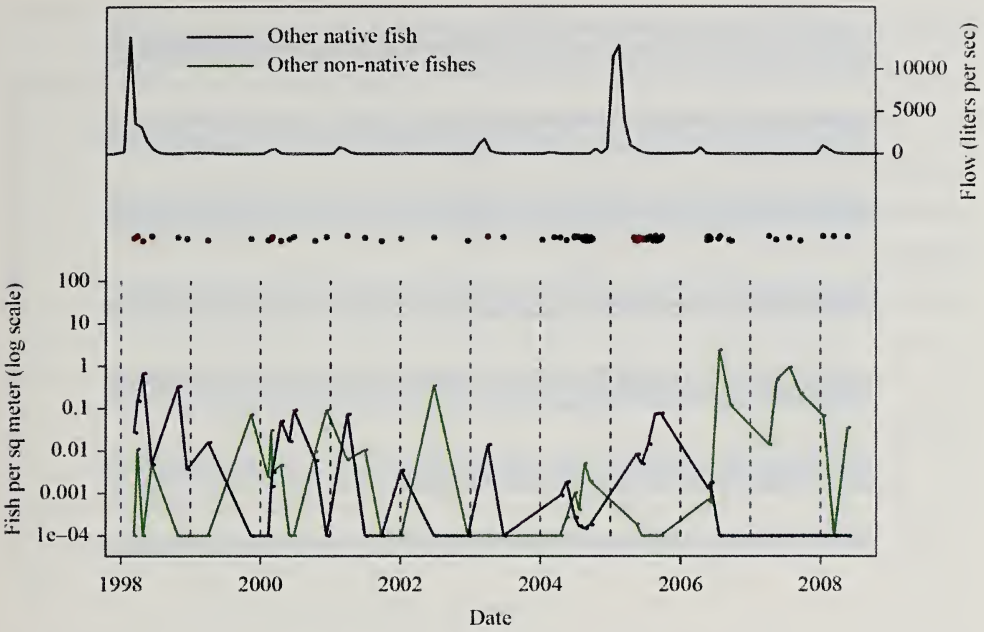

Fig. 9. Abundance of native and non-native species at San Mateo Lagoon, 1998-2008 excluding the southern tidewater goby (native) and mosquitofish (non-native). Dotted vertical lines represent January 1st of each year.

Four non-native freshwater fish species came down to the lagoon during the two high rainfall periods, largemouth bass, green sunfish, bluegill, and black bullhead. Largemouth bass reproduced and proliferated in the lagoon in 1998-99 and were extirpated with seines while southern tidewater gobies were absent. One adult bluegill was taken on March 30, 2001 near the lagoon-stream interface. The black bullhead and green sunfish came down both times and remained uncommon or absent from 1998 to 2004. From 2004-2008 green sunfish and black bullhead slowly increased in numbers with successive dry years and became abundant through the end of the study in 2008.

Cluster analysis on the number and presence/absence of the 12 most common species (excluding longjaw mudsucker, bluegill, reef surfperch, arrow goby, and yellowfin goby) resulted in two groups (Fig. 10). One group is a stepwise series of nested associations largely dictated by the relative frequency of the species in all samples. The second group is the strong association of southern tidewater goby and mosquitofish, the two species most abundant and consistently present in both wet and dry seasons. Additional clusters (not shown) utilizing all species (including the rare ones) as well as separating the data into two-time periods bracketing the separate high flow events with slightly different species compositions (1998-2003; 2004-2008) also resulted in similar dichotomies; the southern tidewater goby and mosquitofish strongly associated and separate from the remaining estuarine and freshwater species prevalent during wet seasons. In both time periods the wet season/lagoon opening periods include both the invading estuarine species and freshwater species from upstream. During the intervening dry years, the estuarine species declined or disappeared and the southern tidewater goby, mosquitofish and, from 2004-2008, two non-native freshwater species, green sunfish and black bullhead, proliferated.

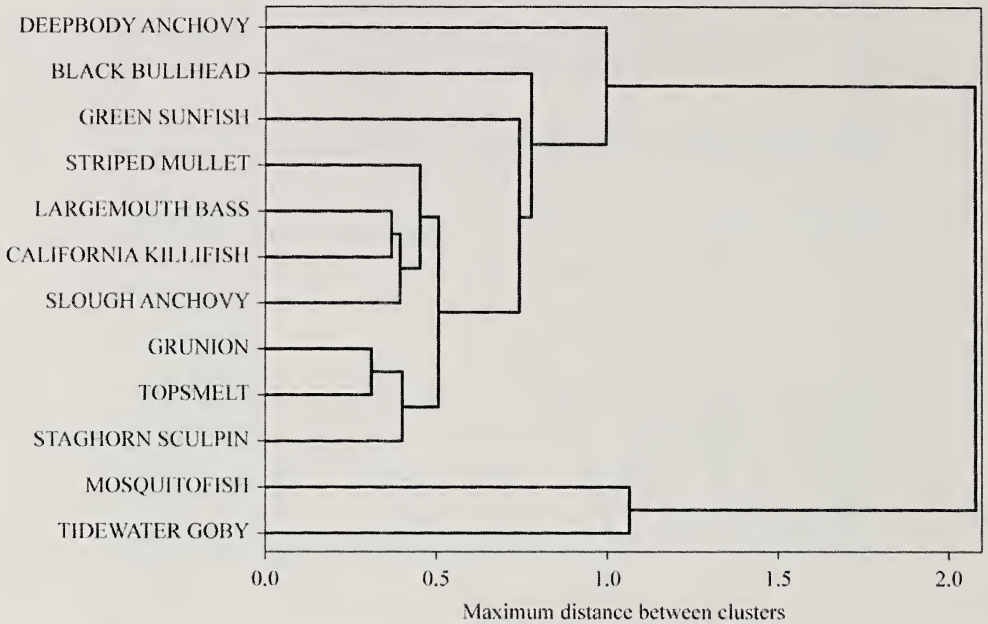

Fig. 10. Cluster analysis with hierarchical clustering with complete linkage of the fish species collected in seine samples, excluding five rarest species (see text).

Two other non-native aquatic species, bullfrog, *Rana catesbiana* and red swamp crayfish, *Procambarus clarki*, were common at the beginning of the study and were decimated during the high 1998 El Niño flows. They increased in abundance through 2004 when active removal efforts began. Catches of both species declined through 2008; the bullfrogs were essentially eliminated but crayfish remained in lower numbers.[1,2]

The 100-200 m of perennial tributary upstream of the lagoon usually supported large numbers of juvenile southern tidewater goby and mosquitofish and fewer green sunfish and black bullhead. On November 26-27, 2001 the removal effort took 1648 juvenile to adult southern tidewater gobies (about 14.5 gobies/m^2) and a few hundred each of mosquitofish and red swamp crayfish. On 8 February 2002 124 southern tidewater gobies came from 93 m of the new channel with about the same number of mosquitofish crayfish.

Discussion

When open the lagoon became at least partially tidal. Deep initial gaps scoured through the sand berm usually lasted only days during peak flows and the bar quickly began to reform. Surf action kept the breach in the barrier sand bar relatively high and shallow, muting the tidal fluctuation. Tidal influence progressively became restricted to the periods of highest spring tides in the middle of the night about every two weeks (grunion tides). At lower

[1] ENTRIX, Inc. 2007. Results of exotic predator removal efforts from San Mateo Lagoon and creek from 9 April to 20 September 2007. Report for CalTrans via EDAW, Inc., San Diego, Project Number 3049906, 23 pp.

[2] ENTRIX, Inc. 2008. Final Report. Results of exotic predator removal efforts in San Mateo Creek and lagoon between 16 January to 23 May 2008. Report for Caltrans via EDAW, Inc., San Diego, Project Number 3049908, 44 pp.

tides the lagoon stabilized with little or no outward flow and some seepage through the berm. After complete closure, the lagoon level became elevated a meter or so above mean high tides. Marine water occasionally washed into the lagoon through the lower level of the sand berm at the former outlet when high surf occurred during nocturnal highest tides. The progressively widening of the barrier berm into the summer reduced the ability of waves to wash over and the lagoon level stabilized about a meter or more above mean high tide. Some seepage through the barrier sand bar and evaporation contributed to the lagoon level slowly declining during the dry season or over successive dry years. The lagoon was reduced to one hectare or less by 2008 and was observed by Swift and Holland to become reduced in size also by the early 1990s after the dry period spanning the late 1980s and early 1990s.

Estuarine coastal lagoons or estuaries that close to the ocean to some extent have recently been labelled variously as: 1) temporary open/closed estuaries (TOCE) (Whitfield et al. 2012; Collins and Melak 2014); 2) intermittently open/closed estuaries (IOCE) (McSweeny et al. 2017); 3) intermittently closed and open lakes or lagoons (ICOLL) (Sadat-Noori et al. 2016); or, 4) intermittently closed estuaries (ICE) (Moreira et al. 2015) and are prevalent in coastal areas with Mediterranean climate regimes like the west coast of North America. Jacobs et al.'s (2011) historical research and classification of these systems in southern California concluded that only a few of the largest California estuaries like San Diego and San Francisco bays were consistently open to the sea. As we have observed and Jacobs et al. (2011) determined San Mateo Lagoon is a highly enclosed system perched above high high tide as the predominant condition on a terraced coastline facing southwesterly and exposed to southerly and El Niño storms on an isolated medium-sized coastal drainage. This places it at the largely closed, fresh or brackish water end of a spectrum that extends to systems rarely or never completely closed with strong marine or saline influence. However, as we have observed, San Mateo Lagoon transitions over a few weeks or months from a marine influenced system to its "predominant" closed and fresh or brackish condition during wet years. Artificial modifications and development has converted many systems that were similar to San Mateo farther towards increased tidal and marine conditions. Unlike many other sites closely fringed with development, San Mateo Lagoon currently has relatively unfettered ability to expand inland with sea level rise, an accommodation not available at many other sites.

The geographical location of the lagoon in the coastal belt of summer fog makes the highest local air temperatures often in spring and fall when more sunlight is present (Leighly 1934; Patton 1956; Purer 1942). This depression of summer air temperatures often does not show up in the typically averaged monthly air temperature data. The summer fogs diminish summer solar impacts, which are stronger in fall and spring and combine to make the water temperature often cooler than the local ocean in summer and warmer than the ocean in the winter. The lagoon water temperature often varies less than in the nearby marine environment when lagoons are closed or nearly so. Sudden cooling can occur in winter when the lagoon opens to the colder ocean simultaneously with incoming stream flows cooled by exceptionally cold air.

The water temperature records at San Mateo did not show any reduction in mid-summer as documented in the more tidal Ballona Marsh.[3] At San Mateo water

[3] Swift, C.C. and G.D. Frantz. 1981. Estuarine fish communities of Ballona. 31 pp. in Biota of the Ballona Region Los Angeles County (R. Schrieber, ed.), Natural History Museum of Los Angeles County, Los Angeles.

temperature rose to the low to mid-20°s C in mid to late summer and the two to four values measured from the lower and upper lagoon and creek usually differed less than 3-5° C from each other. Still some shaded areas of the lagoon under the railroad trestle remained cooler, i.e. in the lower rather than mid-20°s C. The creek temperatures were similar to the lagoon in the early years of the study since the riparian vegetation had been removed and exposed the creek. In later years as the riparian vegetation redeveloped the ground water fed creek was several degrees cooler in the summer rarely above 20° C (Fig. 7).

The fluctuations of fish populations at San Mateo Lagoon corresponded to the cycles of two near record wet periods separated by stretches of near record dry years. Wet years opened the lagoon and allowed native estuarine species to enter from the ocean like topsmelt and the two species of anchovies that spawned in the lagoon. Large numbers of adult grunion occasionally were trapped in the lagoon after washing in during nocturnal high tides in spring. They feebly swam at the surface near the seaward end of the lagoon, apparently stressed by low salinity exposing then to predation by larger tern species. Four other estuarine fish species entered as larvae or small juveniles and did not reproduce, longjaw mudsucker, striped mullet, staghorn sculpin, and arrow goby. A ninth species, california killifish, typically inhabit more tidal estuaries and occur sparsely along sandy coasts. They invaded the lagoon and even reproduced on one occasion. The surfperch rarely strayed into the lagoon from the rocky substrate just off the mouth of the lagoon. All of these disappeared or remained as rare adults during intervening dry periods. The southern tidewater goby was the only native species that maintained large numbers during the dry periods when the lagoon was mostly closed or opened only briefly.

Non-native species also increased with the wet years with the yellowfin goby entering as small juveniles during lagoon opening but only surviving as a handful of adults in the closed lagoon after the 2005 wet year. Green sunfish, largemouth bass, and black bullhead came down from upstream during the first wet season and the sunfish and bullhead only were recorded during the second. They remained rare after 1998 probably because the lagoon was strongly flushed out in early 1998 and lacked vegetative cover. Also, in early 2000 the smaller lagoon experienced an artificial opening and resulting high salinity event that was probably detrimental to them. After 2005 the green sunfish and black bullhead increased in numbers through 2008 despite efforts to remove them. The lagoon retained considerably marginal emergent vegetation providing cover for these two species. The many juvenile largemouth bass present in the latest 1990s were removed successfully by the time southern tidewater gobies were re-introduced in January 2000. Predation by the increased number of sunfish and bullhead catfish almost certainly caused the extirpation of the southern tidewater goby by mid-2007. The larger gobies (longjaw mudsucker, yellowfin goby) and staghorn sculpin could prey on southern tidewater goby but very few survived in the closed fresh or brackish conditions of the closed lagoon. Yellowfin goby and staghorn sculpin live for at least several months in freshwater farther north (Moyle 2002). Our record for large longjaw mudsucker in the lagoon indicate it is equally tolerant despite Barlow's (1961) contention it could survive only about two weeks in fresh water. The one goldfish taken during frog removal efforts was obviously a recent unauthorized release.

In 1996 and 1998–2001 the seven other lagoons to the south on the base were sampled one to four times per year and similar increases in number of fish species were recorded

during the 1998 El Niño.[4,5] Six of these lagoons north to south (San Onofre, Las Flores (Las Pulgas on some maps), Hidden, Aliso, French, and Cockleburr) were about the same size or smaller than San Mateo, had similar fish faunas, and also lost some of the estuarine species after one or two years. San Onofre and Las Flores with relatively large freshwater input returned to fresh or brackish condition similar to San Mateo. The other four lagoons with smaller drainage basins and reduced freshwater input often retained considerable salinity along with some estuarine species like longjaw mudsucker, staghorn sculpin, arrow goby and few others not recorded in San Mateo like shadow goby, *Quietula y-cauda*, cheekspot goby, *Ilypnus gilberti*, and diamond turbot, *Pleuronichthys guttulatus*. Hidden and French often became hypersaline and French typically dried to a small hypersaline and fishless pool within a salt flat during the stretches of dry years. The much larger and southernmost lagoon on MCB, the Santa Margarita River, usually had all the above species except southern tidewater goby that disappeared in the early 2000s. In addition, grey smoothhound, *Mustelus californicus*, round stingray, *Urobatis halleri*, california butterfly ray, *Gymnura marmorata*, bat ray, *Myliobatis californica*, and the rare southern invader, longtail goby, *Ctenogobius sagittula*, were taken. In 1999 two striped bass, *Morone saxailis*, were taken during the colder oceanic La Niña conditions that brought an increased notice of catches of this species in the anecdotal angler records in the regional newspaper Western Outdoor News. A small population of another southern estuarine species, the Pacific blue crab, *Callinectes arcuatus*, also was present in the Santa Margarita for about a year and a half in 1998-99, was not seen subsequently, but was again present in January 2009 (Swift, personal observation, LACM specimens). The Pacific blue crab and longtail goby apparently had not been able to establish reproducing populations up through 2009.

Ambrose and Meffert (1999) and Collins and Mellack (2014) extensively describe and compare the patterns of fish community variation in small TOCE's both in southern California and elsewhere in Mediterranean climate regions. Diversity is typically lowest in nontidal or microtidal systems mostly brackish or freshwater with a few brackish specialists like the southern and northern tidewater gobies in California. Increased tidal action and salinity with rising frequency and depth of openings supports progressively more species and diversity of estuarine and marine species, many using the estuary as a nursery. Some or all of these dominated the fish communities in other more tidal and saline southern California estuaries (Allen et al. 2006) except tidewater gobies and steelhead that have been greatly reduced or extirpated in many of the more saline and tidal systems.

Two additional native fishes, partially armored threespine stickleback, *Gasterosteus aculeatus microcephalus,* (last recorded in 1939) and southern steelhead, *Oncorhynchus mykiss* (Swift et al. 1993; Hovey 2004; Hubbs 1946) previously occurred or traversed San Mateo Lagoon but were not taken in this study. Genetic evidence showed at least 5 steelhead entered San Mateo Creek and spawned upstream in 1998 (Hovey 2004). Their progeny also reproduced in a tributary creek but dry conditions in subsequent years prevented the adults

[4] Swift, C.C., and D.C. Holland. 1998. The status and distribution of the tidewater goby, *Eucyclogobius newberryi* (Pisces, Gobiidae), on MCB Camp Pendleton, California. Final Rept., Environmental Security, Marine Corps Base Camp Pendleton, CA Contract No. M0068196T5642, 104 pp.

[5] Holland, D.C., C.C. Swift, and N. Sisk. 2001. Status, distribution, and habitat use of the tidewater goby, *Eucyclogobius newberryi* (Teleostei: Gobiidae), on MCB Camp Pendleton, California, California 1998-2001. Final Report for AC/S Environmental Security, MCB Camp Pendleton, AS, by Camp Pendleton Amphibian and Reptile Survey, Fallbrook, CA, Contract #M00681-00-P-1347.

from returning to the sea as well as the out migration of their offspring to the ocean. The population declined and disappeared by late 2003 (Hovey 2004). Steelhead utilized seasonally stable, brackish or fresh lagoon, and were commonly fished up to 1930s as "sundowners" in southern California coastal lagoons (Hubbs 1946; R. Croker, letter, quoted in Swift et al. 1993). Studies in central California have shown the value of lagoon habitats in allowing the young steelhead to reach larger sizes increasing their success in returning to spawn after their time in the ocean (Satherwaite et al. 2012). Historically the drainage supported more steelhead during periods of wet years and Rodgers (1889) observations and Woefel's (1991) detailed research show the stream was more consistently present all year in the lowland valley above the lagoon before about 1940. Subsequently the transition from dry farming to irrigated vegetables in the floodplain above the lagoon and other water needs made increased demands on the water table of the alluvial valley and stream flow became much less prevalent. The irrigated farming in the drainage ended in 2001 and may lead to increased water in the stream. Partially armored threespine stickleback were probably also affected by loss of flows in the lower creek as well as by predation by the non-native predatory fish and crayfish.

Tidewater gobies were recorded initially in San Mateo Lagoon 1940 (UMMZ 133246) and next in 1974 (Swift et al. 1989). They could not be detected in the mid to late 1980s (Robert Feldmuth, pers. comm., 23 March 1987[6]; Swift visit, 31 August 1988) a period of extended drought. They were absent in 1991[7] but were present and rare in 1993.[8] They remained present and sometimes abundant until March 1998 when extirpated as noted above. Repeated sampling failed to detect them through late 1999 and after their reintroduction in January 2000 they remained present and often abundant through mid-2007 (Fig. 8, Appendix I). They could no longer be found from mid-2007 through mid-2008, apparently extirpated by increasing numbers of non-native predators (sunfish, bullheads) that proliferated in a closed, freshwater lagoon. They were not recorded again until 2010 (Kevin Lafferty, pers. comm.) apparently naturally recolonized after our sampling through mid-2008.

Northern and southern tidewater gobies are characteristic of coastal lagoons, but where habitat remains suitable and accessible they invade low gradient tributary streams. The 100-200 m of perennial tributary upstream of San Mateo Lagoon usually supported large numbers of juvenile tidewater goby and mosquitofish and fewer green sunfish and black bullhead. Farther south on the base southern tidewater goby (≤ 10) were taken up to 3-4 km above the lagoon in the Santa Margarita River on 6-8 June 2000 (Holland, pers. obs.). Large numbers (at least hundreds) of northern tidewater gobies, *Eucyclogobius newberryi*, moved 7-8 km upstream in the Santa Ynez River in the summer and fall, coincident with upstream movement of juvenile staghorn sculpin and starry flounder, *Platichthys stellatus*

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[6] Feldmeth, C.R., D.A. Guthrie, D.L. Soltz, B.A. Prigge, and W.J. Bond. 1987 (April 25). Draft Biological Resources of the San Mateo Creek area, Camp Pendleton. Robert C. Feldmuth and Associates, Ecological Research Services, Claremont, CA, for Natural Resource Office, Camp Pendleton, CA, Contract No. M00681-85-Q-0048, 139 pp.

[7] Holland, D.C. 1992. The distribution and status of the tidewater goby (*Eucyclogobius newberryi*) on Camp Pendleton, San Diego County, California. Environmental and Natural Resources Office, Marine Corps Base Camp Pendleton, California.

[8] Swift, C.C., J.N. Baskin, T.R. Haglund. 1994. The status and distribution of the tidewater goby, *Eucyclogobius newberryi* (Pisces: Gobiidae), on MCB Camp Pendleton, California. Marine Corps Base Camp Pendleton, Report for Contract # M0068193-P-4385.

in 1995-1997.[9] Tributaries can provide nursery habitat for tidewater gobies where accessible, but today many coastal lagoons have natural or artificial barriers to such movement. Rodgers (1889) observed the San Mateo Valley "...is notable as one of the few through which a well-organized running stream may be seen above the surface, the year round." Possibly this just referred to the lower few hundred meters as we have observed, but the water table was probably higher historically and more consistently supported a surface stream along the 7-8 km of low gradient floodplain upstream of the lagoon (Woefel 1991).

Removal of abundant bullfrog larvae seemed to allow greater growth of green algae in the lagoon, and historically, the larvae of the native and federally threatened California redlegged frog, *Rana aurora draytoni*, now locally extirpated[10] (Jennings and Hayes 1994), may also have reduced the algae. The federally endangered arroyo toad, *Bufo californicus* was present and larvae and small juveniles were present in the upper lagoon during the two wet years. They successfully bred locally during these wet years since the strong flows exposed shallow marginal gravel bars they prefer for breeding. They were not detected in other dryer years in and near the lagoon. The southwestern pond turtle, *Clemmys marmorata*, was present throughout the study.

Bullfrogs and crayfish were reduced by seining and trapping. Local populations of southwestern pond turtles, cormorants, black crowned night herons, great blue herons, great egret, snowy egret, and kingfishers also targeted fish and crayfish in the lagoon. The crayfish declined in numbers, but some remained using the vegetation as a refuge from capture and predation. Bullfrogs adults, larvae, and egg masses were targeted from 2004 to 2008, and were essentially extirpated in the local area.[11,12] Occasional adults taken probably immigrated from adjacent drainages or from upstream areas outside the study area. San Mateo Lagoon is relatively isolated by unsuitable habitat for these two species. Concerted effort on complete drainages followed by continued follow-up could largely eliminate or greatly reduce them in many areas. This effort should be targeted to periods immediately or soon after high flow events when the species have been naturally decimated and the open habitat condition makes the species vulnerable to removal methods. A few ($\leq$10) red eared sliders, *Trachemys scripta*, were taken in 2004-2008 while trapping for non-native fish and were removed from the lagoon.

Historical maps and accounts of early travelers and residents (Rodgers 1889; Woefel 1991; Engstrom 1999, 2006; Grossinger et al. 2011) indicate a wider and larger San Mateo lagoon extending inside and parallel to the sand dunes before the railroad crossing was built. The lagoon was further restricted in the 1930s when levees were established to protect

[9] Swift, C.C., P. Duangsitti, C. Clemente, K. Hasserd, and L. Valle. 1997. Biology and distribution of the tidewater goby, *Eucyclogobius newberryi*, on Vandenberg Air Force Base, Santa Barbara County, California. Final Report, U.S. National Biological Survey Cooperative Agreement No.1445-007-94-8129 with Loyola Marymount University, Los Angeles, 121 pp.

[10] Holland, D.C. and R.H. Goodman, Jr. 1998. A guide to the amphibians and reptiles of MCB Camp Pendleton, San Diego County, California. Report for AC/S Environmental Security, Marine Corps Base Camp Pendleton, Contract M00681-94-C-0039, by Camp Pendleton Amphibian and Reptile Survey, Fallbrook, CA, v + 546 pp.

[11] ENTRIX, Inc. 2007. Results of exotic predator removal efforts from San Mateo Lagoon and creek from April 9 to September 20, 2007. Report for CalTrans via EDAW, Inc., San Diego, Project Number 3049906, 23 pp.

[12] ENTRIX, Inc. 2008. Final Report. Results of exotic predator removal efforts in San Mateo Creek and lagoon between January 16 and May 23, 2008. Report for Caltrans via EDAW, Inc., San Diego, Project Number 3049908, 44 pp.

the new Highway 1 bridge (today's Old Road Bridge), deflecting the stream from the marsh towards the larger, northern railroad bridge (Celia Kutcher, pers. comm., 10-14 September 2014, via discussions with Paul Campo of Marine Corps Base, Camp Pendleton in the 1970s). The lagoon is now restricted to a narrower, linear lagoon almost perpendicular to the shore (Fig. 1). The area and volume of the lagoon was considerably larger and high flows were not channeled directly towards the ocean. A wider lagoon and more marginal wetlands were available to absorb higher flows and the breaching or outlet channel would often be diverted southward along the coast by longshore currents and wave action.

The original lagoon would have been shallow (1-2 m) like today because sediments more or less spread evenly across the lagoon. The resistance of lagoon margins causes slightly more scouring such that the lagoons are often 10-20% deeper on the margins than over most of its area away from the banks. A broad shallow configuration allows wind-driven circulation to keep the water column well oxygenated and prevents or minimizes development of deeper pockets that trap saline water. Saline lenses differentially absorb solar radiation becoming warmer and anoxic. These conditions drive intolerant species of fishes, amphibians, reptiles and other organisms out of deeper water into shallows and more vulnerable to predators. Narrowing of the lagoon also inhibits the deflection or migration of the outlet down the coast where the effects of breaching are much less than when a deep opening is directly scoured as an extension of the main channel.

We observed, and the State Park staff and others have related on a few occasions at San Mateo and other coastal lagoons, bullfrog larvae, crayfish, and bullhead catfish have littered the local beaches soon after high flows breach of the lagoon in the wet season. The native southwestern pond turtles often get washed out as well. During a similar even on nearby San Onofre Lagoon we observed gulls picking up bullfrog larvae but losing interest soon after apparently due to their toxic skin. The high salinity along the beach leads to extensive mortality of these freshwater species. The pond turtles and crayfish crawl out of the surf back towards the lagoon, but some beach goers, believing these are young lobsters and sea turtles, attempt to return them to the ocean. During the strong opening and mixing of fresh and saline water in the lower lagoon 17 May-16 June 2005 10-20 moribund southern tidewater gobies and windrows of dead aquatic insects were present along the lower lagoon. Swift et al. (1989) showed southern tidewater goby, while tolerant of a wide range of salinity, had more difficulty adapting to rapid, strong changes in salinity.

In addition to these natural winter breaching events, mortality of native and non-native aquatic species can result from a sudden, artificial breaching of a lagoon in the dry season (Swift, et al., pers. obs.). Periodic dry season opening of the lagoon for public health reasons, along with the lagoon at San Juan Creek to the north, began when the State Park was established in 1971 (C. Kutcher, personal communication, see above) but was later curtailed to protect the native aquatic species. Some surfers believe opening lagoons provides a fresh sand deposition just offshore enhancing the surf break at this famous surfing beach ("Upper trestles"). These artificial breaches are timed with extreme low tides to maximize the draining and sediment movement. This also maximizes the effects on lagoon inhabitants when there is little or no freshwater inflow to refill the lagoon. Sometimes summer openings are made to remove pollution, excess algae build up, or perceived adverse odors but then can add to the bacterial count in local beach water. Farther north coastal lagoons have been breached to facilitate entry of anadromous salmonids in the fall or winter before natural openings occur. The lowering of lagoon levels whether natural or artificial often forces fishes and other organisms out of marginal protective vegetation.

Changes in the vegetative cover affected the survival of fish populations. Sudden lowering of water levels exposes fish to predation since they lose access to marginal vegetative cover. During our study this marginal aquatic vegetation also prevented complete control of non-native exotic predators but was beneficial for many native organisms, some now locally extirpated. However, historically Native American populations also impacted this vegetation. In August 1856 while passing by San Mateo Lagoon Hayes (1929: 117) noted "Much of the tule here had been cut by the Indians for their various uses." This portrays a substantial local effect on marsh vegetation that may have been typical for many California coastal marsh habitats every fall, or possibly even more frequently, for the last few thousand years.

Conclusions

Historically San Mateo lagoon supported more native fishes and amphibians with increased and consistent freshwater inflow and a larger lagoon. Like Ambrose and Meffert (1999) at Malibu Lagoon, our sampling did not take the federally endangered southern steelhead known to have passed through the lagoons in both systems during the studies. Although a small steelhead run remains at least intermittently in both drainages, neither lagoon appears to support southern steelhead recruitment. Both could be restored enough for this function to return. Lagoons may have been relatively more important for steelhead in southern California given the smaller and less persistent freshwater tributaries compared to more northern localities. Such restoration would also benefit threespine stickleback, red-legged frog, arroyo toad, southwestern pond turtle, and southern tidewater goby.

An overall long-term trend of reduction and confinement of coastal lagoons including San Mateo as noted above needs to be reversed to increase the suitability for the suite of native aquatic species. Despite the apparent decrease of freshwater inflow from the creek, San Mateo lagoon stays fresh, brackish, or nearly so most of the time. The lack of dams or other sediment diversions means sediments continue to be delivered to the lagoon providing material for the building of barrier sand berms by coastal wave action. The lagoon should be allowed or restored to a broader footprint closer to its original extent. The elevated railroad berm and the levees confining the channel inhibit natural expansion of the lagoon laterally and also block the more or less continual wind that helps mix and oxygenate the lagoon waters. Confinement into a narrower channel allows high flows to scour deeper channels that inhibit complete wind-driven mixing of the water column as well, making it easier for saline lenses to develop. Channelized high flow place more force directly against the barrier berms increasing the extent and duration of breaches to the ocean instead of dissipating them laterally down coast where outlet channels remain shallower and higher in the tidal range. Such muted breaching allows interchange of fishes but retains more of the lagoon intact in contrast to the more severe direct scouring that can nearly or completely drain the system. Even just seasonal flooding of lateral lagoon margins provides valuable refuge for native fishes during high scouring flows. Restoration of coastal lagoons and their historical fauna and flora will necessitate reversing these trends by reproducing or simulating historical conditions as much as possible. Preventing artificial breaching has been part of such management and educational efforts to discourage, manage or prevent artificial breaching as well as to improve water quality and supply in these coastal habitats should be continued.

Habitat changes must be accompanied by management or removal of exotic competitors and predators that we have seen can thrive under some conditions. Strong

circumstantial evidence indicates steelhead, threespine stickleback, both species of tidewater goby, and small juvenile southwestern pond turtle are negatively impacted by non-native predators, including largemouth bass, sunfish, bullheads, and bullfrogs. Lafferty and Page (1997) showed African clawed frog, *Xenopus laevis,* also preyed on northern tidewater goby in the Santa Clara River estuary. Various life stages of these non-native animals can both by direct prey on native species as well as compete for resources. Red swamp crayfish also have strong effects on amphibian eggs and larvae along with the other non-native species in southern California (Riley et al. 2005). Bullfrogs appear easiest to control at San Mateo because of the vulnerability of the adults and the egg masses. Targeting them led to virtually complete removal save for occasional immigration. The exotic freshwater fish are more difficult once established since they have much inaccessible habitat for protection. Success was achieved with largemouth bass since they were more vulnerable immediately and soon after flood scouring of the lagoon that removed much of their cover. Crayfish removal is much harder to accomplish and with freshwater fishes should probably be concentrated after exceptional flood conditions when they are very reduced as well as identifying upstream sources that can be controlled or removed.

Steelhead can reinvade the San Mateo drainage under favorable conditions, but it is very unlikely stickleback or redlegged frog could naturally recolonize. Like southern tidewater goby they would have to be artificially brought in from the most genetically suitable populations. Normally this would require at least a few hundred individuals to assure genetic viability (USFWS 2005). Such reintroductions should not be carried out until the habitat is considered favorable including the reduction or elimination of the known and suspected incompatible non-natives.

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Appendix I

Dates, seine hauls, area seined, fish catches and condition of lagoon opening to ocean for San Mateo Lagoon, 1993-2008. Numbers in species columns and total fish column represent actual counted and estimated catches. Columns of both total native and total non-native species include numbers based on multiples indicated in "Multiplier" column for southern tidewater goby and mosquitofish numbers (see Methods).

Date (mm/dd/yr)	Number of hauls	Area m^2	Multiplier (see text)	Native fishes											Non-native fishes									
				Southern Tidewater Goby	Arrow Goby	Longjaw Mudsucker	Staghorn Sculpin	Deepbody Anchovy	Slough Anchovy	California Killifish	Striped Mullet	Topsmelt	Grunion	Reef Surfperch	Yellowfin Goby	Mosquitofish	Largemouth Bass	Black Bullhead	Green Sunfish	Bluegill	Total fish	Total native fish	Total non-native fish	Closed (1); open (2)
10/14/93	24	329	1	24	0	0	0	0	0	2	0	0	0	0	0	300	0	0	0	0	326	26	300	1
10/20/96	16	333	1	1323	0	0	0	0	0	0	0	0	0	0	0	824	0	3	0	0	2150	1323	827	1
03/11/98	15	555	1	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	15	15	0	2
03/28/98	12	180	1	0	0	0	0	0	0	2	25	0	0	0	0	0	0	2	0	0	29	27	2	2
04/26/98	20	300	1	0	0	0	0	0	0	0	204	0	0	0	0	0	0	0	0	0	204	204	0	2
06/11/98	34	1039	1	0	0	0	0	0	0	0	3	2	0	0	1	0	3	1	0	0	10	5	5	1
10/27/98	21	783	1	0	0	0	0	0	259	0	5	0	0	0	0	86	0	0	0	0	350	264	86	1
12/12/98	14	548	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1
04/02/99	32	877	1	0	14	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	30	14	16	2
11/13/99	24	1597	1	0	0	0	0	0	0	0	0	0	0	0	0	70	114	0	0	0	184	0	184	1
02/11/00	32	1280	1	5	0	0	0	0	0	0	0	0	0	0	0	6	2	1	0	0	14	5	9	1
02/26/00	17	680	1	0	0	0	0	0	0	0	1	0	0	0	0	25	2	19	0	0	47	1	46	2
03/03/00	49	1263	1	3	0	0	0	0	0	4	0	0	0	0	0	1500	1	3	0	0	1511	7	1504	2
04/17/00	38	1520	1	0	0	0	27	0	0	0	0	10	40	0	0	100	0	7	0	0	184	77	107	2
05/31/00	24	360	1	101	0	0	6	0	0	0	0	0	0	0	0	1200	0	0	0	0	1307	107	1200	1
06/23/00	24	360	1	54	0	0	15	0	0	18	0	0	0	0	0	550	0	0	0	0	637	87	550	1
10/13/00	21	840	1	95	0	0	5	0	0	0	0	0	0	0	0	2500	0	8	0	0	2608	100	2508	1
12/11/00	19	285	1	323	0	0	0	0	0	0	0	0	0	0	0	1160	0	26	0	0	1509	323	1186	1
03/30/01	22	330	1	568	0	0	14	0	0	0	10	0	0	0	0	59	0	1	0	1	653	592	61	2
06/30/01	12	191	1	2158	0	0	0	0	0	0	0	0	0	0	0	410	0	2	0	0	2570	2158	412	1
09/25/01	19	190	1	1887	0	0	0	0	0	0	0	0	0	0	0	745	0	0	0	0	2632	1887	745	1
01/04/02	19	285	1	450	0	0	1	0	0	0	0	0	0	0	0	300	0	0	0	0	751	451	300	1
06/25/02	29	435	1	483	0	0	0	0	0	0	0	0	0	0	0	500	0	150	0	0	1133	483	650	1
12/19/02	24	588	1	10	0	0	0	0	0	0	0	0	0	0	0	150	0	0	0	0	160	10	150	1

				Native fishes											Non-native fishes									
Date (mm/dd/yr)	Number of hauls	Area m^2	Multiplier (see text)	Southern Tidewater Goby	Arrow Goby	Longjaw Mudsucker	Staghorn Sculpin	Deepbody Anchovy	Slough Anchovy	California Killifish	Striped Mullet	Topsmelt	Grunion	Reef Surfperch	Yellowfin Goby	Mosquitofish	Largemouth Bass	Black Bullhead	Green Sunfish	Bluegill	Total fish	Total native fish	Total non-native fish	Closed (1); open (2)
04/02/03	19	285	1	44	0	0	1	0	0	0	0	3	0	0	0	3	0	0	0	0	51	48	3	2
06/23/03	8	120	1	1600	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	0	1629	1600	29	1
01/13/04	13	325	1	92	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	107	92	15	1
03/15/04	38	1388	2	635	0	0	2	0	0	0	0	0	0	0	0	595	0	0	0	0	1232	1272	1190	1
04/14/04	36	1124	1	2474	0	0	1	0	0	0	0	0	0	0	0	2093	0	0	0	0	4568	2475	2093	1
05/17/04	41	3728	7	1176	0	0	7	0	0	0	0	0	0	0	1	469	0	0	0	0	1653	8239	3284	1
06/28/04	15	225	1	2625	0	0	0	0	0	0	0	0	0	0	1	450	0	0	0	0	3076	2625	451	1
06/30/04	29	4191	2	600	0	0	3	0	0	0	0	0	0	0	1	342	0	0	0	0	946	1203	685	1
07/14/04	17	1640	9	300	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	304	2700	28	1
07/19/04	19	2070	9	51	0	0	1	0	0	0	0	0	0	0	0	60	0	0	0	0	112	460	540	1
07/29/04	18	1844	7	70	0	0	0	0	0	0	0	0	0	0	0	378	0	2	0	0	450	490	2648	1
08/04/04	46	1448	5	124	0	0	0	0	0	0	0	0	0	0	0	4864	0	4	0	0	4992	620	24324	1
08/12/04	12	1968	9	1	0	0	0	0	0	0	0	0	0	0	0	19	0	15	0	0	35	9	186	1
08/18/04	13	1440	9	27	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	47	243	180	1
08/23/04	13	1440	9	15	0	0	0	0	0	0	0	0	0	0	0	34	0	15	0	0	64	135	321	1
08/25/04	14	1580	9	17	0	0	0	0	0	0	0	0	0	0	0	26	0	40	0	0	83	153	274	1
08/31/04	17	1880	9	79	0	0	2	0	0	0	0	0	0	0	0	45	0	60	0	0	186	713	465	1
09/02/04	15	3220	9	59	0	0	0	0	0	0	0	0	0	0	0	14	0	45	0	0	118	531	171	1
09/07/04	16	2364	1	50	0	0	1	0	0	0	0	0	0	0	1	21	0	20	0	0	93	51	42	1
09/09/04	13	1244	9	20	0	0	0	0	0	0	0	0	0	0	0	26	0	15	0	0	61	180	249	1
09/14/04	17	1580	9	13	0	1	0	0	0	0	0	0	0	0	0	40	0	20	0	0	74	118	380	1
09/21/04	16	2095	9	32	0	0	0	0	0	0	0	0	0	0	0	18	0	20	0	0	70	288	182	1
09/23/04	15	3555	9	28	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	51	252	207	1

Date (mm/dd/yr)	Number of hauls	Area m^2	Multiplier (see text)	Native fishes											Non-native fishes								
				Southern Tidewater Goby	Arrow Goby	Longjaw Mudsucker	Staghorn Sculpin	Deepbody Anchovy	Slough Anchovy	California Killifish	Striped Mullet	Topsmelt	Grunion	Reef Surfperch	Yellowfin Goby	Mosquitofish	Largemouth Bass	Black Bullhead	Green Sunfish	Bluegill	Total fish	Total native fish	Total non-native fish	Closed (1); open (2)
09/28/04	19	2290	9	142	0	1	0	0	0	0	0	0	0	0	0	28	0	0	0	0	171	1279	252	1
09/30/04	20	2420	9	73	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0	108	657	315	1
05/05/05	28	1176	1	98	0	0	25	1	0	0	0	0	0	0	0	3	0	1	0	0	128	124	4	2
05/12/05	46	1932	9	26	0	0	2	0	0	1	0	0	0	0	0	1	0	0	1	0	31	237	10	2
05/17/05	38	1596	9	105	0	0	7	0	0	0	1	0	0	0	0	0	0	0	0	0	113	953	0	2
05/18/05	49	2058	9	8	0	0	2	16	0	0	0	1	0	6	0	0	0	0	0	0	33	97	0	2
05/23/05	30	1260	9	1	0	0	0	2	0	0	0	13	0	2	0	0	0	0	0	0	18	26	0	2
05/24/05	46	1932	9	13	0	0	0	15	0	0	0	8	0	0	0	0	0	0	0	0	36	140	0	2
06/01/05	38	1596	9	10	0	0	1	40	0	3	0	0	1	0	0	1	0	0	0	0	56	135	9	2
06/16/05	27	1134	9	2	0	0	1	32	0	0	0	15	0	0	0	2	0	0	0	0	52	66	18	2
06/20/05	30	1260	9	3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	6	27	27	2
07/11/05	26	1092	9	8	0	0	1	4	0	0	0	4	0	0	0	4	0	0	0	0	21	81	36	1
07/13/05	41	1722	9	3	0	0	0	15	0	0	0	2	0	0	0	2	0	0	0	0	22	44	18	1
07/27/05	30	1260	9	11	0	0	4	36	0	4	0	1	0	0	0	29	0	0	0	0	85	144	261	1
08/11/05	35	1470	9	19	0	0	1	128	0	3	0	0	0	0	0	112	0	0	0	0	263	303	1008	1
08/25/05	28	1176	9	51	0	0	0	147	0	3	0	0	0	0	0	127	0	0	0	0	328	609	1143	1
08/30/05	33	1386	9	10	0	0	0	49	0	0	0	0	0	0	0	24	0	0	0	0	83	139	216	1
09/09/05	40	1680	5	215	0	0	1	212	0	0	0	1	0	0	0	669	0	0	0	0	1098	1289	3345	1
09/20/05	46	1932	5	15	0	0	0	87	0	10	0	0	0	0	0	976	0	0	0	0	1088	172	4880	1
09/27/05	45	1890	4	95	0	0	0	138	0	0	0	0	0	0	0	904	0	0	0	0	1137	518	3616	1
05/22/06	26	908	8	33	0	0	5	0	0	0	0	2	195	0	0	16	0	0	0	0	251	466	128	1
05/23/06	49	1243	9	259	0	0	0	0	0	0	0	0	0	0	0	31	0	0	0	0	290	2331	279	1
05/31/06	21	83	1	202	0	0	0	0	0	0	0	0	0	0	0	151	0	3	0	0	356	202	154	1
06/05/06	23	140	1	516	0	0	0	0	0	0	0	0	0	0	0	186	0	1	2	0	705	516	189	1

Date (mm/dd/yr)	Number of hauls	Area m^2	Multiplier (see text)	Native fishes											Non-native fishes													
				Southern Tidewater Goby	Arrow Goby	Longjaw Mudsucker	Stagehorn Sculpin	Deepbody Anchovy	Slough Anchovy	California Killifish	Striped Mullet	Topsmelt	Grunion	Reef Surfperch	Yellowfin Goby	Mosquitofish	Largemouth Bass	Black Bullhead	Green Sunfish	Bluegill	Total fish	Total native fish	Total non-native fish	Closed (1); open (2)					
06/06/06	12	502	9	2300	0	0	3	0	0	1	0	0	10	0	0	59	0	0	0	0	2373	20714	531	1				
06/07/06	8	480	9	25	0	0	1	0	0	0	0	0	0	0	0	11	0	0	0	0	37	226	99	1				
07/19/06	11	440	1	143	0	0	0	0	0	0	0	0	0	0	0	1325	0	502	167	0	2137	143	1994	1				
07/27/06	4	65	1	43	0	0	0	0	0	0	0	0	0	0	0	900	0	110	130	0	1183	43	1140	1				
09/13/06	5	300	9	100	0	0	0	0	0	0	0	0	0	0	0	200	0	0	25	0	325	900	1825	1				
09/26/06	9	90	1	300	0	0	0	0	0	0	0	0	0	0	0	200	0	0	15	0	515	300	215	1				
04/09/07	18	360	9	30	0	0	0	0	0	0	0	0	0	0	0	31	0	0	5	0	66	270	284	1				
05/18/07	24	240	9	3	0	0	0	0	0	0	0	0	0	0	0	313	0	0	114	0	430	27	2931	1				
07/24/07	27	270	1	0	0	0	0	0	0	0	0	0	0	0	0	250	0	0	250	0	500	0	500	1				
09/20/07	29	290	1	0	0	0	0	0	0	0	0	0	0	0	0	252	0	0	65	0	317	0	317	1				
01/16/08	15	225	1	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	15	0	25	0	25	1				
03/12/08	7	350	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1				
05/22/08	20	200	1	0	0	0	0	0	0	0	0	0	0	0	0	23	0	0	7	0	30	0	30	1				
				22,478	14	2	140	922	261	51	264	62	246	8	6	26,966	122	1096	796	1	53,435								

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Investigating the Disappearance of Short-finned Pilot Whales (*Globicephala macrorhynchus*) from Southern California: Did Fisheries Play a Role?

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Abstract.—There is a mystery surrounding the disappearance of short-finned pilot whales (*Globicephala macrorhynchus*) from southern California. This species was very common in these waters through the early 1980s, with an apparently seasonally-resident population centered around Santa Catalina Island in the Southern California Bight. From 1980-1985, pilot whale numbers off Catalina Island declined dramatically, and they eventually disappeared. One theory has been proposed for this phenomenon, suggesting that a strong El Niño event in 1982/83 resulted in a failure of their main prey, market squid (*Doryteuthis opalescens*), which lead to their departure. However, we argue that previously underestimated impacts from fishery by-catch and other anthropogenic effects may have actually been the primary driver. Information from diverse sources show that from the 1950s to 1980s, pilot whales were subject to extensive by-catches in purse-seine nets, lampara nets, and oceanic driftnets, as well as intentional shooting by fishermen, and live-captures for the aquarium industry. As a result, dozens of animals may have been removed in some years. From 1952 to 2014, we have documented no less than 232 individuals removed from southern California, with >52% through known anthropogenic factors. If these removals primarily affected the Catalina Island 'residents', they would have had a severe impact on that population. We conclude that human interactions of various types almost certainly played an important, and previously unrecognized, role in the disappearance of short-finned pilot whales from southern California waters.

One of the great mysteries in American marine mammal biology has to do with the short-finned pilot whale (*Globicephala macrorhynchus*) population or populations in southern California. This species has been known from the southern California and Baja California coasts for over a century, and in 1920 Nidever (1921) reported a school of about 100 near Santa Catalina Island (hereafter referred to as "Catalina Island"). The species was common in southern California waters through the mid-1980s, and a "resident population" was thought to occur around Catalina Island in the southern California Bight (SCB) (Leatherwood et al. 1973; Walker 1975; Dohl et al. 1981). Around 1983/1984, a dramatic decline in their numbers was evident, and they essentially disappeared from California waters. Since that time, short-finned pilot whale sightings have been infrequent and broadly distributed along the coast, rather than concentrated near Catalina Island (Barlow and Forney 2007; Kendall-Bar 2015; Kendall-Bar et al. 2016). In the space of a few short years,

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Fig. 1. Short-finned pilot whales observed off Palos Verdes, California, in December 1986, showing distinctive features used in photo-identification. Photo by A. Schulman-Janiger.

they went from being one of the most common cetacean species in southern California to being essentially absent.

Focal studies of the species documented this disappearance (Shane 1995a), but only one explanation has been offered for this unprecedented event. The hypothesis was advanced that the pilot whales moved away in response to the 1982/83 El Niño, which disrupted the annual squid (*Doryteuthis opalescens*) spawning around the Channel Islands, on which the pilot whales apparently depended for food. According to this theory, an influx of Risso's dolphins (*Grampus griseus*) then moved into the area and occupied the pilot whales' teuthophageous niche, thereby inhibiting the pilot whales from returning (Shane 1991; 1995a,b). Several points have been offered in support of this hypothesis (see discussion below), but there are other alternative explanations that have not been fully considered.

The El Niño theory was never proven and it was never determined where the pilot whales may have gone (Fig. 1). Despite the increase in surveys along the U.S. West Coast and the coast of Baja California, Mexico (Barlow and Forney 2007; Wade and Gerrodette 1993, Ferguson and Barlow 2003; Hamilton et al. 2009), no areas with pilot whale concentrations of a similar magnitude have been documented. Besides the above-mentioned El Niño and associated effects, there were a number of other changes and activities happening in southern California at the time that the pilot whales disappeared. Our goal in this paper is to re-examine this issue, and to consider the potential role that fisheries interactions may have had in the pilot whales' vanishing. We will proceed by reviewing published and unpublished information (supplemented with new data and analyses) on several aspects of the biology of these animals in southern California.

Materials and Methods

Pilot whale stock structure information for southern California and also for the entire eastern North Pacific was examined through review of both published and unpublished

Table 1. Strip transect estmates of density and abundance of short-finned pilot whales within 15 km of Santa Catalina Island (data from Oliver and Jackson 1987). D = individual density, N = abundance.

Time period	Years	Agency*	Surveys	Effort (nm^2)	Groups sighted	D (#/nm^2)	N	CV
1	1980/81	CDFG	15	1,575	167	0.9744	300	0.50
2	1982/83	NMFS	9	1,049	43	0.4004	123	0.23
3	1983/84	NMFS	6	850	0	0	0	n/a
4	1984/85	NMFS	5	710	2	0.0887	27	2.95
5	Late 1985	NMFS	2	242	1	0.0372	11	n/a

* CDFG = California Department of Fish and Game; NMFS = National Marine Fisheries Service.

literature. Distribution of short-finned pilot whales in the SCB was evaluated by creating a database of sightings from historical studies off southern California. To be included, these studies must have conducted systematic searches for cetaceans or compiled pilot whale sightings and have presented either specific positions for the sightings in the form of latitude/longitude coordinates or provided maps of the sightings for which positions could be estimated. Sources of such literature included Fiscus and Niggol (1965) and Norris and Prescott (1961) for the 1950s and early 1960s, Leatherwood et al. (1973), Dohl et al. (1981), and Bonnell and Ford (2001) for the 1970s and early 1980s, Oliver and Jackson (1987) for the 1980s, and multiple cruise reports for surveys conducted by the U.S. National Marine Fisheries Service (NMFS), Southwest Fisheries Science Center (SWFSC) of the U.S. West Coast between 1991 and 2014.

In addition to reviewing available estimates of abundance from the literature, we also used an existing, but unanalyzed, dataset to calculate a new historical estimate of density and abundance for the area around Catalina Island. Strip-transect surveys targeting short-finned pilot whales around Catalina Island were conducted by the California Department of Fish and Game (CDFG), and later by the SWFSC between 1980 and 1985 (Oliver and Jackson 1987). Surveys were conducted from December through March (thus 1981/82 refers to the period of December 1981-March 1982). The surveys used a Cessna 337 Skymaster fixed-wing aircraft, and were flown at an altitude of 500 feet at ground speeds of 90-100 knots. Two observers in rear seats monitored a strip 0.5 nm wide, while the pilot and data recorder occupied the front seats of the aircraft (Oliver and Jackson 1987). We did not have access to the raw data, but we used processed data that were presented in an administrative report (Oliver and Jackson 1987). These data were not previously analyzed to obtain density or abundance estimates. Although there were some inconsistencies in the study areas and survey procedures over the study period, it was possible to obtain approximate estimates of abundance for pilot whales for the study area of 308 nm^2 around Catalina Island, by using strip transect methods. Total numbers of sightings and survey effort for each survey period are shown in Table 1. Density, abundance, and their associated coefficient of variation were calculated as:

$$D = \frac{n\,E(s)}{wL}$$

$$N = D\,A$$

$$CV = \frac{var\,(n/L)}{(n/L)^2} + \frac{var\,[E\,(s)]}{E(s)^2}$$

where D = density (of individuals),

N = abundance,
n = number of sightings made on effort,
E(s) = average group size,
w = width of the survey strip,
L = length of transect completed,
A = size of the study area,
var = variance, and
CV = coefficient of variation.

In order to evaluate and estimate total annual mortality/removals from the SCB, we compiled an Excel table of all known by-catch records, live-captures, and strandings of short-finned pilot whales in California. Stranded specimens that were determined to have died from by-catch after examination were listed as by-catch in the table. "Removal" is here defined as any mortality (natural or anthropogenic), or any physical removal of animals from the population (such as through live-captures). Data came from the published and unpublished literature, as well as records of the Los Angeles County Museum of Natural History (LACM - courtesy of D. Janiger) and the U.S. Navy (courtesy of S. H. Ridgway). As the live-captures were conducted as part of an organized fishery to supply aquaria and research institutes with live cetacean specimens, we consider these removals to be a type of fishery interaction separate from by-catch. We scrutinized and error-checked the database and attempted to eliminate possible duplicate records (see Table 2).

Results and Discussion

The historical stock structure of short-finned pilot whales off California is not well understood; it is currently considered by NMFS that there is a single stock off California/Oregon/Washington (Carretta et al. 2017a). There is an apparent hiatus in distribution centered at around 20°N, which is interpreted to provide evidence that the large number of animals in the Eastern Tropical Pacific (ETP) are from separate populations (Reilly 1977). Multiple stocks are hypothesized to occur in the ETP, but by virtually all accounts, the animals in southern California (and presumably north) were part of a different stock (Reilly 1977; Polisini 1980). This is the so-called "Californian" population center of Reilly (1977) and Polisini (1980). More recent information from Hamilton et al. (2009) suggested that hiatuses in distribution occur at about 18°N and 30°N, providing further support that California animals may be distinct from those in the ETP, and even off southern Baja California, Mexico. However, Forney (1994) questioned whether animals off California were a discrete stock from those in Baja. A recent photo-identification effort revealed that there were several matches from whales off San Clemente Island in 2007 to whales off northern California (offshore of Monterey Bay) in 2008, and to whales in Baja California in 2011; there was also one match between San Clemente Island and northern Baja California in 2015, which suggests that there might actually be a fluid population extending from Baja California northward (Kendall-Bar 2015; Kendall-Bar et al. 2016). Molecular techniques have only recently been applied to the issue of population variation in Pacific pilot whales. Although Van Cise et al. (2016) did not find evidence of strong differentiation in mtDNA control region sequences between California Current and ETP samples, sampling was limited and quite sparse in many cases, and this study therefore does not discount smaller-scale population division.

Although not confirmed through detailed long-term studies, there was a general consensus in the 1970s/80s that there was a resident population (or subpopulation) of pilot whales

Table 2. Documented mortality/removals of short-finned pilot whales in the southern California Bight, 1950-present.

Event #	Date	# Animals	Record type	Location/notes	Reference(s)
1	26-Jul-52	2	Stranding	Imperial Beach (San Diego Cty) - 521 cm M	Danil et al. 2010
2	20-Aug-52	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010, LACM unpubl.
3	23-Jan-54	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
4	9-Feb-56	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
5	6-Feb-57	1	Stranding?	Live capture at Catalina Island - 290 cm M	Norris and Prescott 1961
6	27-Feb-57	1	Capture (live)	Live capture for Marineland ("Bubbles") - young adult 396 cm F	Brown 1960; Norris and Prescott 1961, LACM unpubl.
7	19-Jun-57	1	Capture (live)	Live capture for Marineland ("Squirt")	Gilmore 1962
8	26-Nov-57	1	Stranding	Subadult at Huntington Beach	Norris and Prescott 1961
9	12-Jun-58	1	Stranding	18′3″ male at Torrance Beach	Norris and Prescott 1961
10	21-Jan-59	2	Capture (live)	Live capture for Marineland ("Bimbo") - 524 cm M	Norris and Prescott 1961; Gilmore 1962
11	3-Feb-59	1	Stranding?	San Pedro - 368 cm M	Norris and Prescott 1961
12	8-Feb-59	1	Capture (live)	Live capture - 287 cm M	Norris and Prescott 1961
13	2-Mar-59	2	Capture (live)	Live captured and released - 208 cm F and 275 cm M	Norris and Prescott 1961
14	25-May-59	12	Stranding	Unknown/San Miguel Island	Norris and Prescott 1961
15	25-Jun-59	1	Stranding	Adult at Belmont Shores Beach	Norris and Prescott 1961
16	28-Jan-60	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
17	31-May-60	1	Capture (live)	Live capture S of Pt. Vicente - 263 cm F	Norris and Prescott 1961
18	7-Sep-60	2	Stranding?	San Miguel Island	LACM unpubl.
19	1960	3	Capture (live)	Live captures for Marineland	Gilmore 1962
20	20-Jan-61	1	Stranding?	Long Beach - 381 cm M	LACM unpubl.
21	14-Jun-61	1	Stranding?	Catalina Island	LACM unpubl.
22	9-Mar-62	15	Stranding	San Clemente Island	Mitchell 1965
23	27-Nov-62	1	Capture	San Clemente Island	Rice 1963
24	15-Mar-63	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
25	31-Mar-63	3	Stranding	San Clemente Island	LACM unpubl.
26	28-Aug-63	1	Stranding?	Marineland - 343 cm F	LACM unpubl.
27	15-Mar-65	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
28	31-Aug-66	1	Capture (live)	Live capture for Marineland - 287 cm M	Walker 1975
29	6-Sep-66	1	Capture (live)	Live capture for Marineland - 358 cm F	Walker 1975
30	7-Sep-66	1	Capture (live)	Live capture for Marineland - 320 cm F	Walker 1975, LACM unpubl.

Table 2. Continued.

Event #	Date	# Animals	Record type	Location/notes	Reference(s)
31	18-Sep-66	1	By-catch	By-catch - 197 cm F	LACM unpubl.
32	21-Nov-66	1	Capture (live)	Live capture for Marineland - 340 cm F	Walker 1975
33	23-Nov-66	1	Capture (live)	Live capture for Marineland - 292 cm F	Walker 1975
34	28-Mar-67	1	Capture (live)	Live capture for Marineland - 366 cm F	Walker 1975
35	10-Apr-67	1	Capture (live)	Live capture for Marineland - 292 cm F	LACM unpubl.
36	20-Apr-67	2	Capture (live)	Live captures for Marineland	LACM unpubl.
37	15-Jun-67	1	??	Catalina Channel - 330 cm F	LACM unpubl.
38	27-Jun-67	1	Capture (live)	Live capture for Marineland - 246 cm F	Walker 1975
39	28-Jun-67	1	Capture (live)	Live capture for Marineland - 480 cm F	Walker 1975
40	23-Aug-67	1	Stranding	Unknown	Danil et al. 2010
41	4-Mar-68	1	Capture (live)	Live capture for Marineland - 381 cm F	Walker 1975
42	11-Mar-68	1	Capture (live)	Live capture for Marineland - 320 cm F	Walker 1975
43	?? Oct 68	1	Capture (live)	Live capture for US Navy ("Morgan") - 12′ M	Bowers and Henderson 1972
44	6-May-69	1	Capture (live)	Live capture for Marineland - 290 cm M	Walker 1975, LACM unpubl.
45	9-May-69	1	Capture (live)	Live capture for Marineland - 259 cm F	Walker 1975
46	21-May-69	1	Capture (live)	Live capture for Marineland - 277 cm M	Walker 1975
47	29-May-69	1	Capture (live)	Live capture for Marineland - F	Walker 1975
48	2-Jun-69	1	Capture (live)	Live capture for Marineland - 325 cm M	Walker 1975
49	?? Jul 69	1	Capture (live)	Live capture for US Navy ("Modo")	S. H. Ridgway, pers. comm.
50	17-Sep-69	1	Capture (live)	Live capture for Marineland - 373 cm M	Walker 1975
51	8-Oct-69	1	Capture (live)	Live capture for Marineland - 457 cm F	Walker 1975, LACM unpubl.
52	31-Oct-69	1	??	Santa Barbara - 295 cm M	LACM unpubl.
53	10-Dec-69	1	Stranding/by-catch	Fishery interaction	Hacker 1986; Sinclair 1992
54	26-Dec-69	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
55	??	8-10	Capture (live)	Captured for Sea World, with some mortality	S. H. Ridgway, pers. comm.
56	7-Jan-70	1	Capture (live)	Live capture for Marineland - 310 cm F	Walker 1975
57	18-Jan-70	1	Capture (live)	Live capture for Marineland - 348 cm M (or 310 cm)	Walker 1975, LACM unpubl.
58	22-Jan-70	1	Capture (live)	Live capture for Marineland - 320 cm M	Walker 1975, LACM unpubl.

Table 2. Continued.

Event #	Date	# Animals	Record type	Location/notes	Reference(s)
59	23-Jan-70	1	Capture (live)	Live capture for Marineland - 325 cm M	Walker 1975, LACM unpubl.
60	29-Jan-70	1	Capture (live)	Live capture for Marineland - M	Walker 1975
61	?? Jan 70	1	Capture (live)	Live capture for US Navy ("Pip") - 366 cm M	Bowers and Henderson 1972
62	6-Feb-70	1	Capture (live)	Live capture for Marineland - 320 cm F	Walker 1975, LACM unpubl.
63	3-Nov-70	1	Capture (live)	Live capture for Marineland - 396 cm F	Walker 1975, LACM unpubl.
64	11-Dec-70	1	Capture (live)	Live capture for Marineland - 305 cm M	Walker 1975
65	8-Jan-71	28	Stranding	San Clemente Island mass stranding - 6 M, 21 F, 1 ?	Hall et al. 1971, LACM unpubl.
66	10-Nov-71	1	Capture (live)	Live capture for Marineland - 315 cm F	Walker 1975
67	11-Nov-71	1	Capture (live)	Live capture for Marineland - 326 cm F	Walker 1975
68	2-Feb-72	1	Capture (live)	Live capture for Marineland - 330 cm F	Walker 1975
69	24-Mar-72	1	Stranding?	San Clemente Island	LACM unpubl.
70	21-Nov-72	1	Capture (live)	Live capture for Marineland - 320 cm F	Walker 1975, LACM unpubl.
71	30-Nov-72	1	Capture (live)	Live capture for Marineland - 305 cm F	Walker 1975
72	1-Dec-72	1	Capture (live)	Live capture for Marineland - 351 cm F	Walker 1975; LACM unpubl.
73	12-Dec-72	1	Capture (live)	Live capture for Marineland - M	Walker 1975
74	15-Dec-72	1	Capture (live)	Live capture for Marineland - F	Walker 1975; LACM unpubl.
75	12-Mar-73	1	Stranding	Solan Beach (San Diego Cty) - 453 cm F	Danil et al. 2010; LACM unpubl.
76	15-Mar-73	2	Stranding	La Jolla (San Diego Cty) - 437 cm F	Danil et al. 2010
77	24-Mar-73	1	Stranding	San Clemente Island	LACM unpubl.
78	3-Apr-73	1	Stranding	Camp Pendelton - 434 cm F	LACM unpubl.
79	12-Apr-73	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
80	24-Jul-73	1	Capture (live)	Live capture, San Pedro Channel - 351 cm F	
81	27-May-05	3	Capture (live)	Live-capture	Reeves and Leatherwood 1984
82	15-Oct-75	1	Stranding/by-catch	Fishery interaction (from forensic evidence) - Palos Verdes - 461 cm F	Heyning et al. 1994; Sinclair 1992; Hacker 1986
83	7-Nov-75	1	Stranding/by-catch	Fishery interaction (from forensic evidence)	Heyning et al. 1994; Sinclair 1992; Hacker 1986

Table 2. Continued.

Event #	Date	# Animals	Record type	Location/notes	Reference(s)
84	28-May-05	4	Capture (live)	Live-capture	Reeves and Leatherwood 1984
85	5-Oct-76	1	Stranding	Stranded alive - 249 cm	LACM unpubl.
86	8-Oct-76	1	Stranding	Stranded alive	Otten 1979
87	29-May-05	3	Capture (live)	Live-capture	Reeves and Leatherwood 1984
88	7-Nov-77	1	By-catch	Fishery interaction (caught in anchovy net), LA Cty. - 670 cm M	Heyning et al. 1994; Seagars and Henderson 1985; LACM unpubl.
89	19-Nov-77	2	Stranding/by-catch	Fishery interaction (from forensic evidence), LA Cty. - 419 cm F, 433 cm ?	Heyning et al. 1994; Seagars and Henderson 1985; LACM unpubl.
	22-Nov-77	1	Stranding/by-catch	Fishery interaction (from forensic evidence), Ventura Co. - 422 cm (or 419 cm)	Heyning et al. 1994; Seagars and Henderson 1985; LACM unpubl.
90	23-Nov-77	1	Stranding/by-catch	Fishery interaction (from forensic evidence), Ventura Co. - ca. 430 cm	Heyning et al. 1994; Seagars and Henderson 1985; Hacker 1986
91	16-25 Nov-77	4	Stranding/by-catch	Evidence of fishery interaction and squid in stomachs of some animals	Payne 1978
92	5-Mar-78	1	Stranding?	Manhattan Beach - 447 cm F	LACM unpubl.
93	31-May-05	2	Capture (live)	Live-capture	Reeves and Leatherwood 1984
94	22-Jan-80	1	Stranding/by-catch	Fishery interaction (from forensic evidence), Catalina Island - ca. 500 cm	Heyning et al. 1994
95	2-Nov-80	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
96	5-Dec-80	1	Stranding	Cabrillo Beach	LACM unpubl.
97	17-Dec-80	5	Stranding/by-catch	Fishery interaction, Catalina Island (from forensic evidence)	Heyning et al. 1994
98	19-Dec-80	1	Stranding/by-catch	Fishery interaction (from forensic evidence), Catalina Island - 463 cm F	Heyning et al. 1994, Perrin and Kashiwada 1989
99	1980	12*	By-catch	Entanglement in squid purse seine fishery, Catalina Island	Miller et al. 1983

Table 2. Continued.

Event #	Date	# Animals	Record type	Location/notes	Reference(s)
100	2-Jun-05	3	Capture (live)	Live-capture	Reeves and Leatherwood 1984
101	16/17-Dec-80	6	Stranding	Santa Catalina Island	Seagars and Henderson 1985
102	4-Jun-05	2	Capture (live)	Live-capture	Reeves and Leatherwood 1984
103	1980-83	2	By-catch	Entanglement in CA/OR shark/swordfish driftnet fishery	Hanan et al. 1993
104	29-Jan-83	1	Stranding	San Pedro - 584 cm M	LACM unpubl.
105	12-Feb-85	1	Stranding	Found dead on Catalina Island - 472 cm adult F	Shane FN1
106	??-Jul-85	1	Stranding	Unknown (San Diego Cty)	Danil et al. 2010
107	20-Dec-87	1	Stranding	LA Harbor - 192 cm M	LACM unpubl.
108	3-Jan-88	1	Stranding/by-catch	Fishery interaction (from forensic evidence)	Heyning et al. 1994
109	24-Mar-88	1	Stranding	San Clemente Island - ca. 240 cm	Heyning et al. 1994, LACM unpubl.
110	16-Sep-90	1	Stranding	Silver Strand (San Diego Cty) - 400+ cm	Danil et al. 2010; LACM unpubl.
111	28-Sep-90	1	By-catch	Entanglement in California swordfish/shark driftnet fishery	Julian and Beeson 1998; Hanan 1993; Carretta et al. 2017b
112	28-Aug-92	1	By-catch	Entanglement in California swordfish/shark driftnet fishery	Julian and Beeson 1998; Carretta et al. 2017b
113	Aug-Oct 93	8	By-catch	Entanglement in California swordfish/shark driftnet fishery	Julian and Beeson 1998; Carretta et al. 2017b
114	24-Jun-94	1	Stranding	LA Harbor - 224 cm M	LACM unpubl.
115	9-Sep-97	1^	By-catch	Entanglement in California swordfish/shark driftnet fishery	Barlow and Cameron 2003; Carretta et al. 2017b
116	3-Oct-03	1#	By-catch	Entanglement in California swordfish/shark driftnet fishery	Carretta et al. 2017b
117	25-May-08	1	Stranding	Imperial Beach (San Diego Cty) - ca. 330 cm M	Danil et al. 2010, LACM unpubl.
118	Jan-14	2	By-catch	2 taken in CA swordfish driftnet fishery	Carretta et al. 2017b

* Miller et al. (1983) estimated that the true mortality could be three times as many (i.e., 36 animals).
^ Estimated mortality = 7 (Carretta et al. 2005).
# Estimated mortality = 5 (Carretta and Chivers 2004).

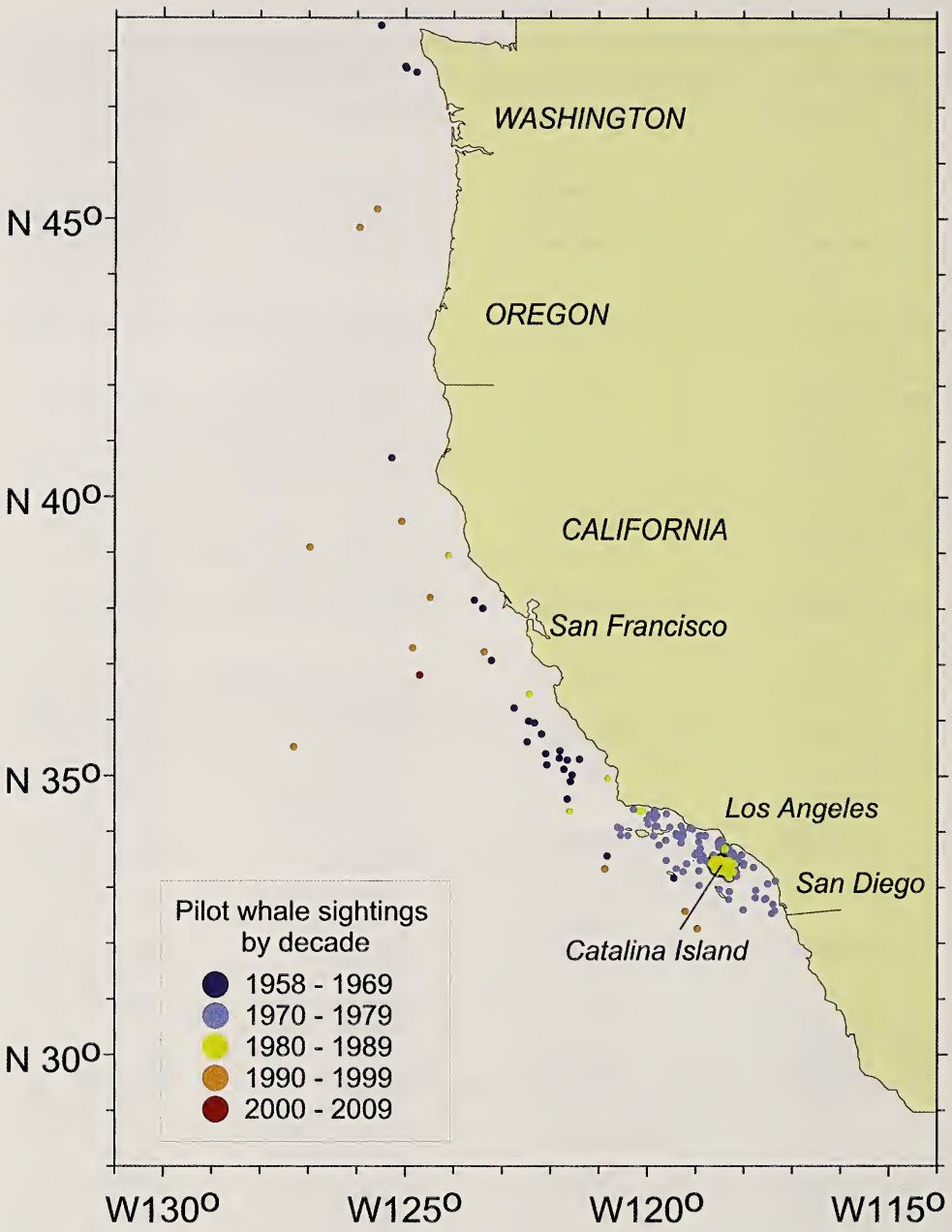

Fig. 2. Map of pilot whale sightings off the U.S. west coast, by decade.

that inhabited the area of the Channel Islands/SCB (including at least Coronado, Catalina, San Clemente, Santa Cruz, Anacapa, and Santa Barbara Islands, the Palos Verdes Peninsula, Pt. Vicente, and Huntington Beach (Leatherwood et al. 1973; Walker 1975; Dohl et al. 1981). The study area, indicating the names of places mentioned, is shown in Figs. 2 and 3. Animals presumably from this population were regularly observed around Catalina Is-

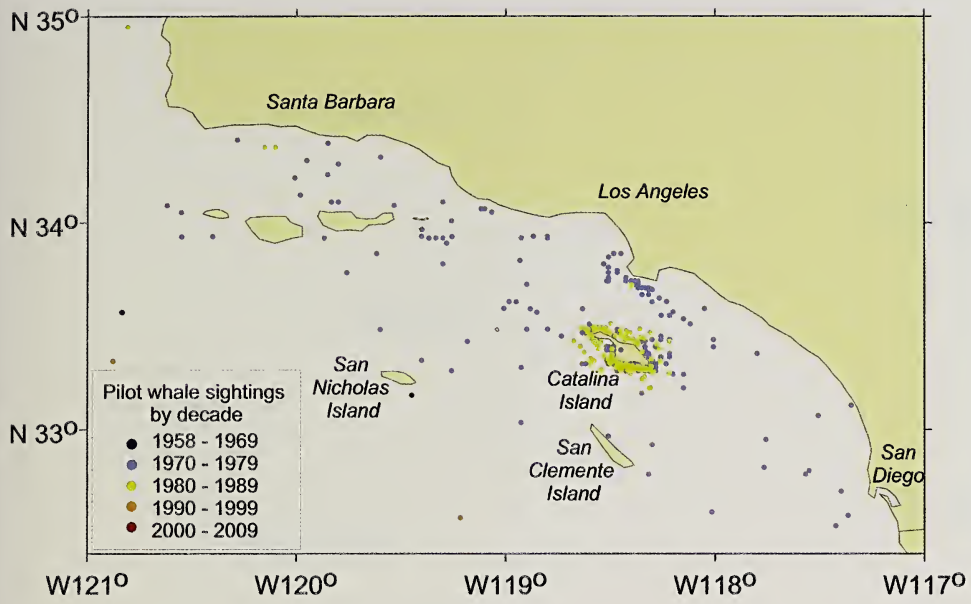

Fig. 3. Map of pilot whale sightings in the Southern California Bight, by decade.

land, especially in winter months, when squid spawn there. Dohl et al. (1981) tagged several individuals with spaghetti and ribbon tags, as well as one with a radio tag. Although relocations were limited, the radio tag data suggested that the animal remained within several tens of kilometers of Catalina Island for at least the one week of data collection. Detailed longitudinal studies of short-finned pilot whales in Hawaiian waters and elsewhere have shown that island-associated populations of this species do occur, and often have strong site fidelity to one or more islands, making them more susceptible to anthropogenic impacts such as those caused by military sonars (Mahaffy et al. 2015).

In spring through autumn months, sightings were more dispersed and were common in offshore waters (Norris and Prescott 1961; Leatherwood et al. 1973; Evans et al. 1984). The whales aggregated each winter, primarily off Catalina Island and the Palos Verdes Peninsula (Figs. 4 and 5). Norris and Prescott (1961) made 46 sightings between the Los Angeles area and Catalina Island in the late 1950s. Some identifiable individuals were seen repeatedly in the 1970s and 1980s (Walker 1975). Focal photo-identification work at Catalina Island (Shane and McSweeney 1990) showed that 32 photo-identified pilot whales were seen at least twice from 1980-1986, but work was cut short by a virtual disappearance of the whales after 1983 (see below). One 'resident' pod of 20 whales was always seen together and never with any other whales from Dec. 1984 to Feb. 1985. Pod stability was considered to be somewhere between the stable groups of killer whales (*Orcinus orca*) and the fission/fusion society of spinner dolphins (*Stenella longirostris*) (Shane and McSweeney 1990).

Although certainly not common, through the 1960s and 1970s, pilot whales were sometimes seen off central California (Brownell 1964; Barham 1982), northern California and Washington (Fiscus and Niggol 1965). There were also records for Oregon and British Columbia (Figs. 2 and 3). Pilot whale distribution in the eastern North Pacific potentially extended as far north as British Columbia (Ford 2014) and even southeast Alaska (Home

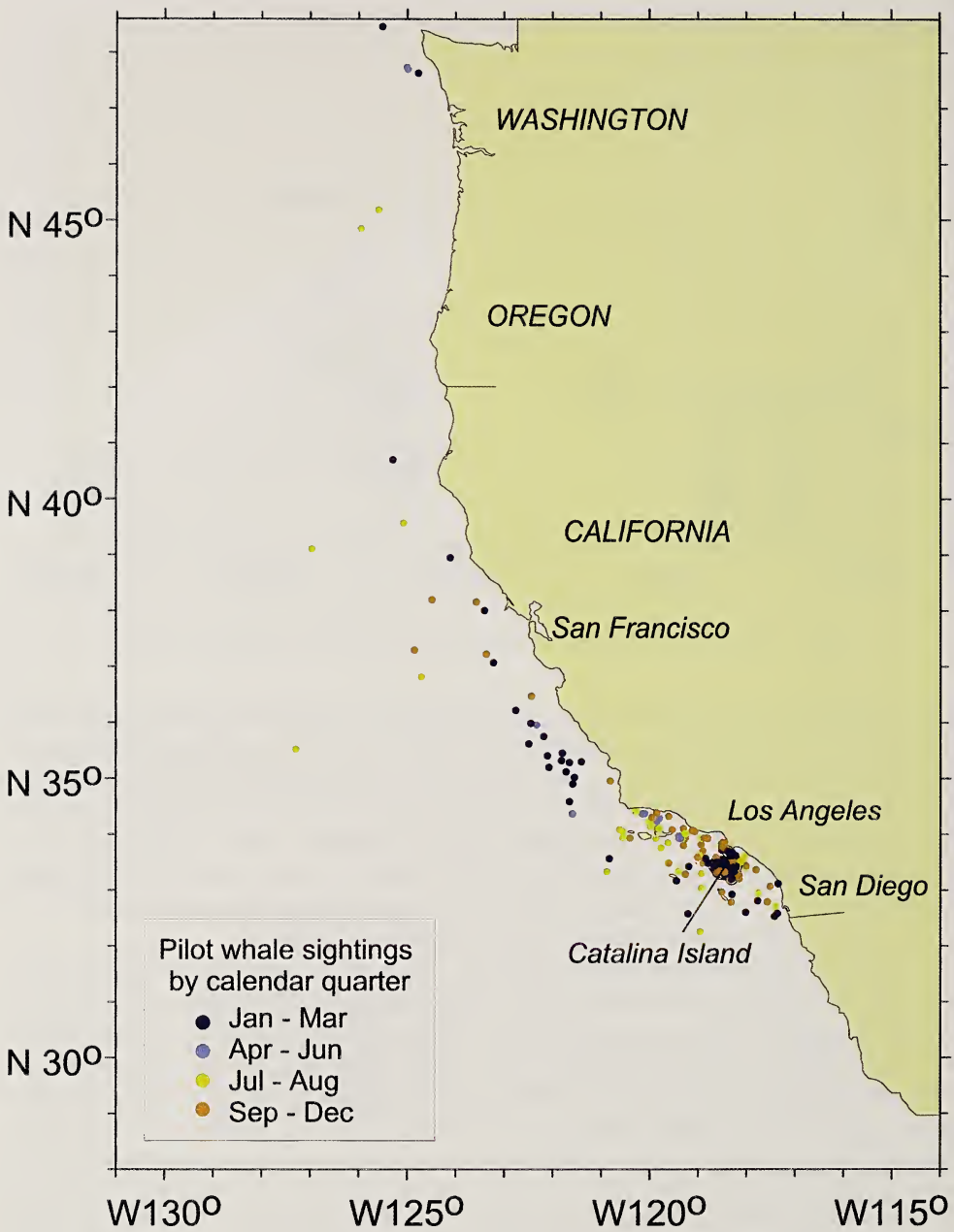

Fig. 4. Map of pilot whale sightings off the U.S. west coast, by season.

1980). In the latter area in 1977, small groups of pilot whales were reported consistently at the mouth of Glacier Bay and around Wrangell Narrows (Home 1980). Pilot whales have been absent from these areas in Alaska throughout the 1990s and 2000s (Dahlheim et al. 2009). Although survey effort has been much lower north of California, and so some of this is effort-related, it is evident that the majority of the animals off western North America

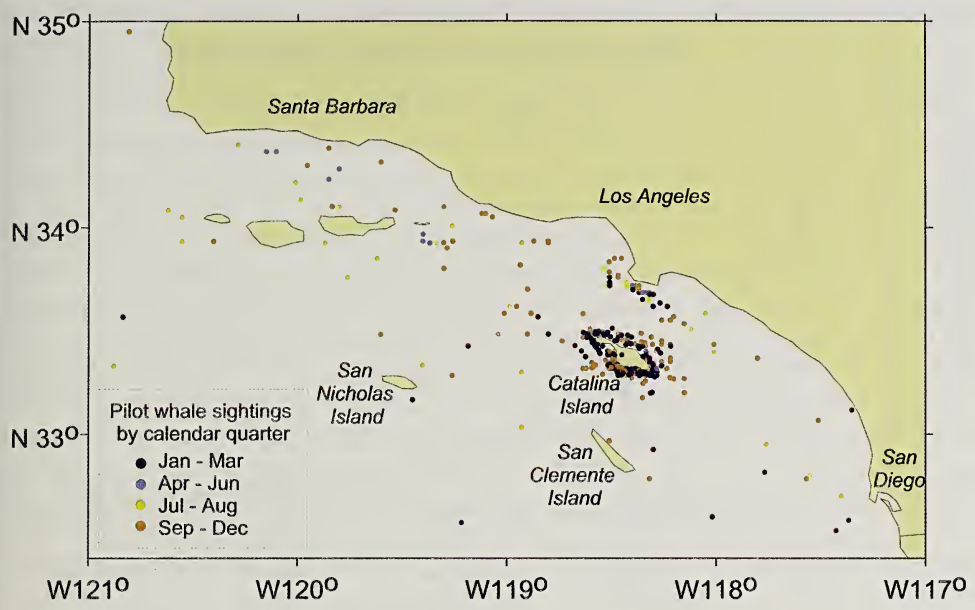

Fig. 5. Map of pilot whale sightings in the Southern California Bight, by season.

traditionally occurred off California. The regions from Oregon to the north were apparently areas of much lower density, with those areas north of the continental U.S. possibly visited only on an extralimital basis (Figs. 2-5).

The published literature contains no reliable, statistically-defensible estimates of historical population size for west coast pilot whales. However, some information can be gained from observations made by various workers in the 1970s and 1980s. On one day in April 1971, two groups estimated at 400 and 100 pilot whales were observed at Catalina Island, and another group of around of 40 was seen at San Clemente Island (Leatherwood et al. 1973). These authors suggested that total numbers probably peaked at over 1,000 whales. Surveys in the late 1970s by Dohl et al. (1981) suggested that the SCB 'resident population' was around 400 individuals, and winter influxes were thought to bring their numbers to about 2,000. However, it must be kept in mind that these were largely educated guesses, and not statistically-derived estimates.

Here we present the results of our new analysis of Catalina Island pilot whale abundance and density in Table 1 and Fig. 6. The results of the strip transect analyses suggest that previous "guesstimates" of the number of pilot whales at Catalina Island were reasonably accurate. For instance, Miller et al. (1983) estimated a maximum of 316 pilot whales at Catalina Island during the squid season in 1980-81. Our estimate for the initial survey in 1980/81 was of 300 individuals (density = 0.9744 animals/nm^2, CV = 0.50), which is very close to that of Miller et al's (1983). Despite high variances, there is strong evidence of a dramatic decline during the short study period of these surveys (Fig. 6, Table 1).

In winter 1983/84, the usual pilot whale aggregation at Catalina Island did not materialize, and this was coincident with the failure of market squid spawning that year, caused by a very strong El Niño event the previous year. Sea surface temperatures (SSTs) at Catalina Island were higher than normal in 1982/83 and 1983/84, then returned to normal

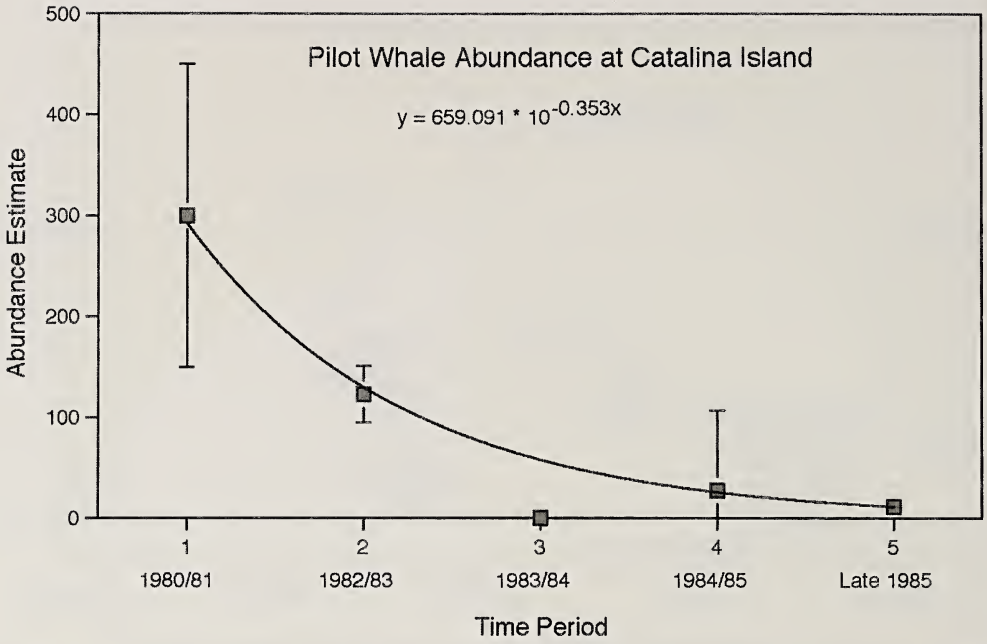

Fig. 6. Strip-transect estimates of abundance for pilot whales around Catalina Island, from CDFG and NMFS aerial surveys (Oliver and Jackson 1987).

in 1984/85[1]. Squid catch went from several thousand tons to just 16 tons, and catch per unit effort dropped dramatically in 1983 and 1984, returning to normal levels in 1985 (Zeidberg et al. 2006). Catch per unit effort was 10-22 tons/vessel day in years before and after, but dropped to near zero in 1983/4 (Zeidberg et al. 2006). The previous year (1982/83), pilot whales were only present from 12 January to 25 February, a very short season.

From 1980-1985, NMFS conducted surveys for pilot whales around Catalina Island. Pilot whales were seen on every flight around Catalina Island in 1980/81 (n = 15), and 1982/83 (n = 9). From December 1983- January 1984, and January 1985 eight flights were conducted, and no pilot whales were seen. Two groups were seen in 7 flights from 1984/85, and only a single group was seen in two flights in December 1985 (Oliver and Jackson 1987). Our strip transect analysis of these data shows a dramatic decline in estimated numbers of pilot whales at Catalina Island from 300 animals in 1980/81 to less than 50 from 1983-1985 (Fig. 6). Although the CVs for these estimates are fairly high (Table 1), the results show a pattern that is consistent with that noted by other researchers, and therefore can be considered somewhat reliable. Interestingly, the abundance estimates show some evidence of a drop in numbers already in 1982/83.

An hypothesis was advanced that pilot whales left Catalina Island in response to reduced squid spawning caused by the 1982/83 El Niño, and that Risso's dolphins came in to fill their niche (Shane 1991). According to this theory, the Risso's dolphins may have actively (aggressively), excluded the pilot whales from coming back (Shane 1991). Both species

[1] Shane, S. H. 1985. Detailed observations of a single pod of pilot whales and sightings of other marine mammals at Catalina Island, California in winter 1984-5. Unpublished report.

mainly feed nocturnally and rest diurnally at Catalina Island, and they both resided in the same areas where market squid were being caught (Shane 1995b). They are both primarily squid-eaters, so this may be an example of competitive displacement (Shane 1995a). Agonistic behaviors by Risso's dolphins toward pilot whales were observed on several occasions, suggesting that aggression was involved (Shane 1995a). If this is true, we do not know where the pilot whales went after leaving Catalina Island. It has been assumed that they moved away[1]. At least six of the pilot whales that were photo-identified off Catalina Island between 1983-1989 were matched to whales photographed across the San Pedro Channel, off the Palos Verdes Peninsula, between December 1986-January 1987 (Shane and McSweeney 1990; Kendall-Bar 2015; Kendall-Bar et al. 2016; ASJ unpubl. data); those group sizes generally varied from 20-30 whales, with perhaps as many as 50 on one day (ASJ unpubl. data). It is possible that pilot whales from the Catalina Island population may have relocated further south into Mexican waters; where there are fewer opportunities for photo captures. However, available photo-identification images taken since 1987 have not shown any matches to the Catalina Island individuals - including images taken off Mexico during ten encounters between 1996-2015 (Kendall-Bar 2015; Kendall-Bar et al. 2016; ASJ unpubl. data). Danil et al. (2010) noted a decrease in pilot whale strandings, associated with the decline in density of this species in the SCB. They suggested some evidence that pilot whales returned to California in later years, but not to the SCB.

Photo-identification and other data do not support the idea that the pilot whales moved north (Shane 1984; Kendall-Bar et al. 2016). Pilot whale records anywhere north of the U.S./Mexico border became rare after this, although a single group was seen offshore south of the San Francisco Bay area in 1991[2]. Five groups of pilot whales were observed on a NOAA survey of the Eastern Tropical Pacific in 1993 (Mangels and Gerrodette 1994). There were just eight published ship-based pilot whale sightings (with photo-IDs) north of Mexico (six in southern California, two in northern California) between 2007-2015; none were off Catalina Island (Kendall-Bar 2015; Kendall-Bar et al. 2016). Aerial surveys in the SCB (much of it around Catalina Island) from 2008-2013 covered 76,989 km and resulted in no pilot whale sightings (Jefferson et al. 2015), and only two pilot whale sightings were made on CalCOFI ship surveys in the SCB covering 25,079 km of effort from 2004-2008 (Douglas et al. 2014). Pilot whale numbers dramatically declined at Catalina Island following the 1982/1983 El Nino, and went from about 100 in 1983, to just a single pod being seen in most years after that, and in some years (1987, 1988, 1990, and 1991) none were seen (Shane 1994).

In the mid- to late-20th century, an extensive live capture fishery occurred to supply Marineland of the Pacific, Sea World, the U.S. Navy, and other institutions with pilot whales for captive display and research (Brown 1960; Norris and Prescott 1961; Walker 1975; Reeves and Leatherwood 1984; Forney 1994). Mortality during and soon after capture was high, and the capture process for this species was particularly difficult, requiring extended periods of time to approach schools to maneuver the hoop net into position for capture (Walker 1975). The captures were mostly from around the Palos Verdes Peninsula and the Channel Islands, so presumably the majority of these pilot whales were from the resident population, which would presumably have caused a great deal of disturbance and

[2] Jones, P. A., and I. D. Szczepaniak. 1992. Report on the seabird and marine mammal censuses conducted for the long-term management strategy (LTMS), August 1990 through November 1991, for the US Environmental Protection Agency. Unpublished report.

stress to the animals (see Walker 1975). Further exacerbating the negative effects of these captures, the majority of the captured animals were females. Of the 50 pilot whales captured between 1966 and 1982 in which sex was reported, 32 (64%) were females (Walker 1975; Reeves and Leatherwood 1984). Our compilation of records indicates that at least 76 individuals were removed from the area through live-captures between 1957 and 1982 (Table 3). Live-captures were especially common during the 1960s and 1970s (Fig. 7). These are known minimums, and since record-keeping was not always consistent (especially before 1972), true numbers were almost certainly higher.

Mortality of short-finned pilot whales in California fisheries is known from at least 1969 (Sinclair 1992). There has been little or no monitoring of most of these fisheries; except for a period of detailed study in the early 1980s (Miller et al. 1983) and recent observation of the swordfish driftnet fishery (Hanan et al. 1993; Carretta et al. 2017a), therefore much of the information comes from stranded specimens with forensic evidence of net entanglement on their bodies. Despite the confounding factor of increased monitoring after 1972 (with the enactment of the Marine Mammal Protection Act), mortality appears to have increased during the 1970s and 1980s (Fig. 7), with pilot whales known to have been killed in several types of encircling net fisheries (i.e., the squid purse seine and lampara net fisheries – together referred to as "round haul" fisheries) and driftnet fisheries (i.e., the California driftnet fishery and California/Oregon swordfish and shark driftnet fishery). Miller et al. (1983, p. 110) stated that the whales were sometimes "wrapped in the purse seine nets and cannot escape". When the net was retrieved by power block, often the tail of the whale would become entangled in the webbing, and the fishermen would cut the tail flukes off, allowing the whale to slip out. This would likely have been fatal to the whale in most cases. Less interaction was thought to have occurred with the dip net fisheries in the Catalina Island area (Miller et al. 1983). A popular account describing these fishery interactions near Catalina Island can be found in Eckert (1970).

In November 1977, at least eight pilot whales stranded in the Los Angeles area, showing some evidence of fishery interaction as a cause of death (Payne 1978). During the same time period, radio transmissions of squid fishermen were intercepted saying that several pilot whales had become entangled in nets and had to be 'beaten and cut' before they could be extracted (Payne 1978). This is suggestive of a serious fisheries interaction problem that had escaped the attention of both state and federal fisheries agents. A particularly damaging year appears to have been 1980, in which 12 pilot whales (a conservative figure) were known to be have been entangled in the squid purse seine fishery around Catalina Island (Miller et al. 1983), and seven pilot whales washed ashore in the Los Angeles area with evidence of fisheries interaction (Heyning et al. 1994). Although based on a small sample, in that year (1980) alone, it is estimated that as many as 60 pilot whales may have been killed as fisheries by-catch (DeMaster et al. 1985). Based on data obtained through a federally-funded marine mammal/fisheries interaction study (Miller et al. 1983), DeMaster et al. (1985) estimated that up to 30 pilot whales may have been taken in squid round haul nets and an additional 30 taken in driftnets. Combined with the 15 known strandings and three live-captures that year, up to 78 pilot whales may have been removed in 1980. If these were all or mostly from a small resident insular population of only a few hundred animals, then this would no doubt have had a catastrophic impact on the stock.

Total by-catch mortality appears to have varied quite a bit from year to year, but as we have shown, in some years it may have been substantial. The sampling of Miller et al. (1983) was limited, and it is very possible that 1980 was not an exceptional year but was more typical of a pattern that was occurring (largely unobserved) in the 1970s/80s. Although pilot

Table 3. Annual known removals of pilot whales from southern California. Note that these are known minimums and the true numbers removed are almost certainly higher.

Year	By-catches	Strandings	Live-captures	Unknown#	Total minimum removals
1952		3			3
1954		1			1
1956		1			1
1957		2	2		4
1958		1			1
1959		14	3		17
1960		3	4		7
1961		2			2
1962		15	1		16
1963		5			5
1965		1			1
1966	1		5		6
1967		1	6	1	8
1968			3		3
1969	1	1	8	1	11
1960s (date unknown)			9		9
1970			9		9
1971		28	2		30
1972		1	6		7
1973		6	1		7
1974			3		3
1975	2		4		6
1976		2	3		5
1977	5	4	0	1	10
1978		1	2		3
1980	19*	8	3		30
1982			2		2
1983	2	1	0		3
1985		2	0		2
1987		1	0		1
1988	1	1	0		2
1990	1	1	0		2
1992	1		0		1
1993	8		0		8
1994		1	0		1
1997	1		0		1
2003	1		0		1
2008		1	0		1
2014	2				2
TOTALS	**45**	**108**	**76**	**3**	**232**

* Miller et al. (1983) estimated that the true number could have been up to 36 animals. DeMaster et al. (1985) estimated that up to 60 pilot whales may have been taken as by-catch in 1980 from combined mortality in squid "round-haul" nets and oceanic gillnets.

Unknown here refers to the type of record (by-catch, stranding, or live capture).

whale population size and status in California was not known, a crude estimate (assuming a population of 300-400 pilot whales off Catalina Island – see Dohl et al. 1981 and Table 1) was that this may have represented 20-26% of the population, and this would certainly have been unsustainable.

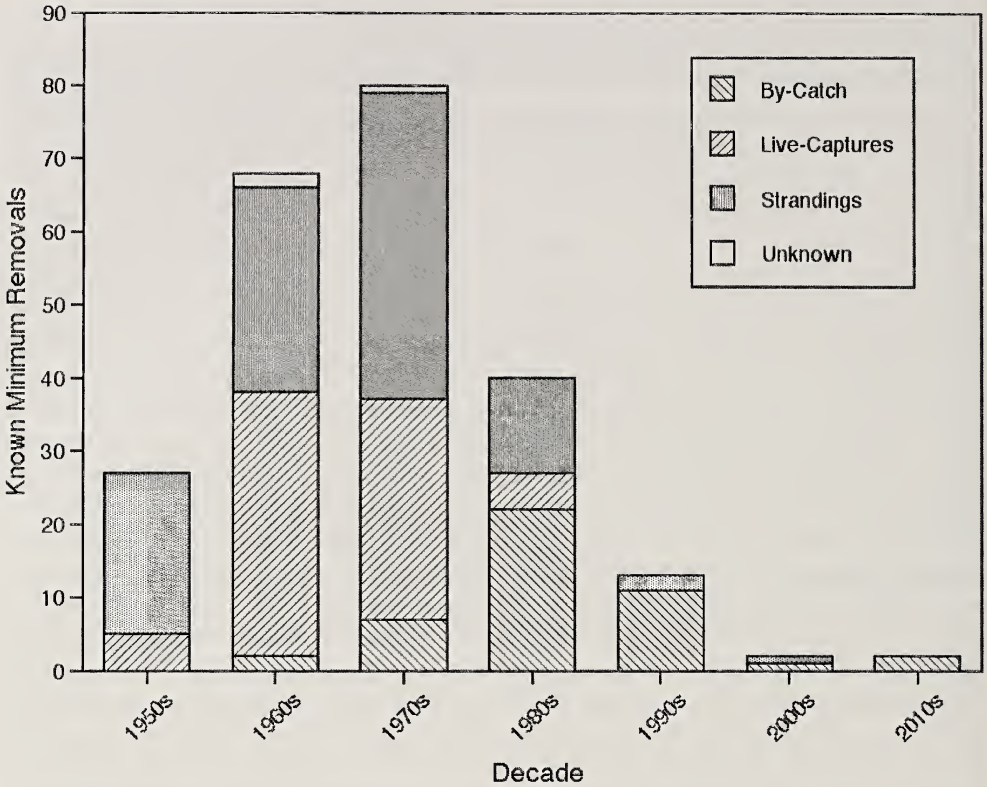

Fig. 7. Minimum levels of removal of pilot whales from southern California by decade. It is important to note that these are not estimates of total removals, which in many cases would likely be significantly higher.

Although occurring mostly outside of southern California (and thus possibly affecting a different, more far-ranging population), high pilot whale mortality in some years appears to have continued through the 1990s and early 2000s. Data from an onboard fisheries observer program suggested that estimated annual mortality of pilot whales in the California swordfish and shark driftnet fishery reached record-high levels of 20 animals in 1990, and 48 animals in 1993 (Lennert et al. 1994; Julian and Beeson 1998; Carretta et al. 2017b). A more recent and improved analysis of these data suggests that approximately 90 pilot whales were taken in the California drift gillnet fishery from 1990-2015 (Carretta et al. 2017b). This was during a time period in which fishing effort was somewhat lower and pingers were being used to reduce by-catch, therefore suggesting that by-catch in the 1980s and before may have been much higher (see Carretta et al. 2017b for details). Clearly, drift gillnet by-catch represents a significant portion of the overall fishery removals for California pilot whales, at least during the 1980s and 1990s. Some mortality also occurred in an experimental flying squid driftnet fishery off British Columbia from 1983-1987 (Jamieson and Heritage 1987, 1988). Based on a small sample of observed vessels, mortality was estimated at 37 pilot whales/year from 1980-1985 (Forney 1994).

Overall, our compilation of records indicates that at least 26 pilot whales were observed taken as by-catch between 1966 and 2014. However, including the animals that were considered to have been killed as by-catch from post-mortem examination, the total comes to

45 individuals, which is also likely an underestimate (Table 3). Observer coverage of these fisheries in the 1960s through 1980s was minimal. In addition, quite a few individuals depicted in the northeastern Pacific Pilot Whale Photo Identification Catalog (Kendall-Bar 2015) display deep and/or encircling scars on their dorsal fins that must have been caused by past entanglements, indicating that this is a serious threat.

Although there are no available estimates of how much mortality this may have caused, it is known that dip net and round haul fishermen regularly shot at pilot whales that drew their ire by coming close to their fishing operations, especially in the purse seine fisheries for squid (Miller et al. 1983). Some squid fishermen felt the pilot whales' presence could be beneficial, but most tended to regard pilot whales as competitors for squid. An acoustic harassment device was tried in early 1982, with apparently no response by the whales (Miller et al. 1983).

In November 1977, coastal residents near Malibu and Point Dume reported hearing shots and explosions (note – the explosions may have been seal bombs, which are known to have been used on marine mammals by fishermen trying to protect their catch and their gear) during the night, at a time when about 400 pilot whales had been reported off the coast (Payne 1978). In December 1980, during the fishery study by Miller et al. (1983), pilot whales were observed near the lights of fishing boats on 35% of the 15-minute observation periods. Miller et al. (1983) stated that "heavy gunfire was noted during December with 156 shots recorded during 15.2 hours of observations" (Miller et al. 1983, p. 108). These represent just two examples of what might have been a common practice at the time.

Although Shane (1994) felt that the shooting was mainly directed at California sea lions (*Zalophus californianus*), it must be assumed that this shooting caused some additional level of mortality for pilot whales, and because the interactions typically occurred at night, they may have easily gone un-noticed. Fishermen claimed that pilot whales sometimes scared the squid away from their nets and even damaged fishing gear, and thus some fishermen had negative feelings toward the whales. Eckert (1970) provided a popular account of the situation around Catalina Island, including a description of the live capture of one animal that died soon afterwards, apparently from having been shot in the head with a 0.38 caliber bullet in an earlier incident.

Conclusions

Despite quite a bit of uncertainty, southern California short-finned pilot whales may have represented a small, vulnerable population associated with the Channel Islands. Strandings have been incompletely documented, but we do know that just three mass strandings occurring in 1959, 1971, and 1980 resulted in the removal of 49 pilot whales from the Channel Islands area. While most strandings are thought to result from natural causes, the area around the southern California Channel Islands is adjacent to a major U.S. Naval base in San Diego, and the possibility that at least some of these strandings were associated with naval sonar must be considered. Both species of pilot whales are prone to mass stranding (Sergeant 1982). A number of mass strandings of deep-diving odontocete cetaceans have been linked to the use of modern low- and mid-frequency active sonar (e.g., Balcomb and Claridge 2001; Southall et al. 2006), which was developed in the 1950s and has been in common use by the Navy in southern California waters for many decades (d'Amico and Pittenger 2009). Pilot whales (*Globicephala* spp.) have been among the species implicated as victims of this technology (Parsons et al. 2008).

Losses from these occasional mass strandings and certain anthropogenic causes (fisheries by-catches, shootings by fishermen, and live captures for aquarium display) may have been affecting the viability of the pilot whale stock since before the MMPA took effect in 1972/73. Although the estimated by-catch for the drift gillnet fishery was approximately 90 individuals between 1990 and 2015 (Carretta et al. 2017b), levels of anthropogenic mortality appear to have reached into the dozens of animals in at least some of the earlier years, and were apparently quite high throughout the 1960s to 1980s (Fig. 7). This could have had a catastrophic effect on a small island-associated population of just a few hundred pilot whales (as has been proposed). We do believe that the 1982/83 El Niño event played a role in their disappearance, but we also think that it was not the only (or even major) factor involved.

Pilot whale sightings off the U.S. west coast have increased recently, some part of this increase is likely due to increases in sighting effort and whalewatching trips in recent years. It is unknown whether these animals are part of a wider-ranging pilot whale population, or if they may represent some individuals from the population that previously was associated with Catalina Island. No photo-ID matches have been made since 1987 to any of the seasonally-resident pilot whales that had been identified off Catalina Island (Kendall-Bar 2015; Kendall-Bar et al. 2016; ASJ unpubl. data). Sightings of pilot whales are still quite rare in the SCB, with no sightings reported off Catalina Island. Squid catches have recovered, and Risso's dolphins (another squid specialist) are still commonly sighted around this island (Jefferson et al. 2015).

If the pilot whales from around Catalina Island represented an extirpated island-associated population, this could explain why pilot whales have not returned to Catalina Island during the past three decades, despite increased regulation of fisheries and low recent levels of documented pilot whale by-catch in all fisheries combined. It is also possible that any surviving pilot whales from this population may have relocated further south into Mexican waters; however, no matches have been made from the available photos taken off Mexico. We therefore conclude that the disappearance of short-finned pilot whales from southern California in the early 1980s was almost certainly caused in part by the mortality of dozens of animals from fisheries by-catches and live-captures, in combination with additional removals from shootings by fishermen (with occasional mass strandings, some possibly anthropogenic, also contributing). If there was indeed a resident island-associated population of short-finned pilot whales in southern California, it might even have been extirpated by these unregulated removals. However, it is possible that another group (or groups) of pilot whales could begin to take up residence in the Catalina Island area, taking advantage of the squid resource, and future research should be directed towards monitoring this possibility.

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Late Quaternary Chorus Frog (*Pseudacris*) from the Channel Islands, California

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Abstract.—Fossil and subfossil remains of the vertebrate faunas from the northern Channel Islands, southern California, have been studied for many decades. Continued interest has focused on skeletal remains of birds, rodents, and mammoths from archaeological and paleontological localities, but considerably less attention has been placed on the detailed description of the herpetofauna (salamanders, anurans [frogs and toads], lizards, and snakes) on the Channel Islands. We present descriptions of an ilium of an anuran from Santa Rosa Island (Larramendy North; radiocarbon dating at least 13,393 calibrated years ago) and two tibiofibulae San Miguel Island (Daisy Cave) dating from earliest and middle late Holocene layers. We identify the fossil ilium as *Pseudacris* sp. (chorus frog): 1) it is the lowest level that skeletal morphology permits us to attempt, 2) realizing that it appears morphologically closest to *P. regilla*, and 3) yet realizing that not all species of *Pseudacris* and *Hyla* have been directly compared or are understood. The extant amphibian fauna on these islands is depauperate. The remains presented here represent the first description of a fossil anuran from the northern Channel Islands. It is now understood that a chorus frog lived on glacial-age Santarosae Island, yet it is not understood when its distribution was reduced to just the present two largest islands, Santa Rosa and Santa Cruz.

Investigation of the Holocene and late Pleistocene terrestrial vertebrate faunas from the northern Channel Islands (NCI) off the coast of Santa Barbara California has received attention for many decades (see discussions in Damiani and Garcelon 2009) (Fig. 1). Of sustained interest has been the analysis of cultural artifacts along with skeletal remains of birds, rodents, and mammoths from archaeological and paleontological localities (e.g., Erlandson et al. 1996; Guthrie 1980, 1998, 2005; Johnson et al. 2002; Ainis and Vellanoweth 2012; Allen 2013; Muhs et al. 2015). What has received considerably less attention other than cursory listings is the detailed assessment of the herpetofauna (salamanders, anurans [frogs and toads], lizards, and snakes). The first and only insular Pleistocene-age salamander (*Batrachoseps*) from the Channel Islands was recovered in association with a late Pleistocene pygmy mammoth (*Mammuthus exilis*; 12,840 ± 140 yr B.P., CAMS-24429, AMS analysis; Agenbroad 1998, 2002; Mead et al. 2004). Here we report on the skeletal remains of the first fossil frog from localities on the NCI: one ilium from Laramendy North, Santa Rosa Island and two leg elements from Daisy Cave A, San Miguel Island.

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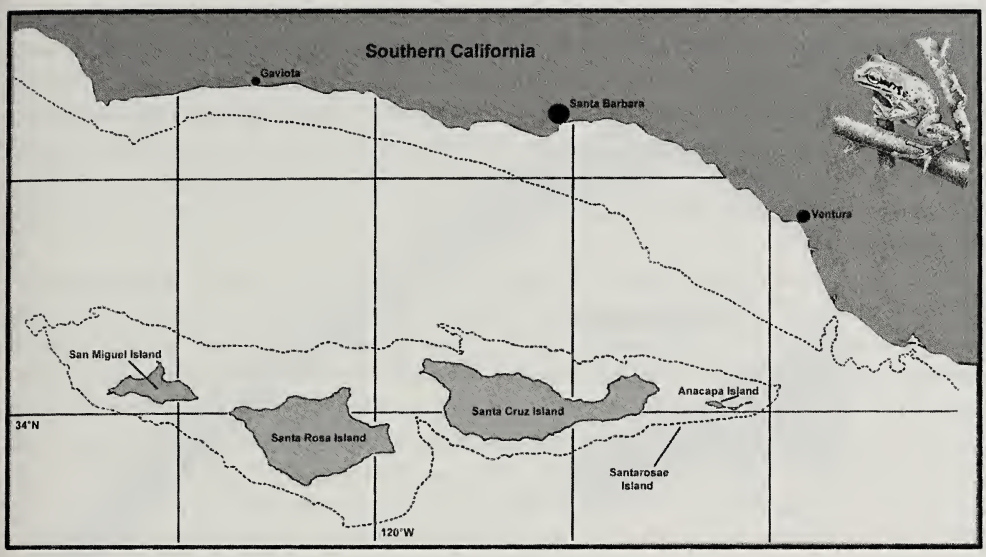

Fig. 1. Map of southern California showing the four islands that make the northern Channel Islands today and the outline of the Santarosae Island that existed with a lowering of sea levels during glacial stands of the Pleistocene. Dotted line denotes lower sea level shorelines. Today *Pseudacris regilla* (see text discussion) is found only on Santa Cruz and Santa Rosa islands, and along the coast of the mainland (see text). Fossil remains *Pseudacris* presented here are found on Santa Rosa and San Miguel islands. Line drawing adapted from Pacifichorticulture.org.

Materials and Methods

Of the multitude of archaeological and paleontological sites on the NCI that have produced microfaunal remains, few have produced remains of amphibians possibly due to collection bias [too large of sieve size used during excavations, e.g., 1.58 mm (1/16"); although see Reddy and Erlandson 2012], or scope of research design not including potential of microfauna such as amphibians. Our sample from San Miguel Island represents sediments partly studied of its microfaunal remains previously sieved through 1.58 mm mesh screens. The specimen from Santa Rosa Island represents a sample recovered from sediments we collected, sieved through 0.5 mm (500 μm) mesh, and sorted with the aid of a light microscope. All specimens were identified using the skeletal comparative collection at The Mammoth Site (Hot Springs, SD) and morphological characters provided in the literature (see discussions below). All specimens belong to the US National Park Service, Channel Islands National Park (CHIS), and are curated by the Santa Barbara Museum of Natural History (SBMNH).

Larramendy North, Santa Rosa Island.—The Larramendy Mammoth site is located in a canyon on the northwestern side of Santa Rosa Island. The general geology of the area is that of alternating alluvial packages of organic-rich clays, silts, sands, and gravels. A mammoth skull was recovered in 2016 from a gravel lens overlain by cross-bedded silty sands and trough cross-bedded sandy gravels. Samples of carbon were recovered from an organic-rich clay above the trough gravels and from a silty sand lens below the gravels, yet all stratigraphically above the mammoth skull. Two radiocarbon dates were obtained above the skull; mean probability ages of 13,106 (USGS 171250, conventional age 11,250 ± 30 yr B.P.) and 13,393 (USGS 171252, conventional age 11,555 ± 35 yr B.P.) calibrated years ago.

Eight meters north of the Larramendy skull is a 15 cm-thick sandy gravel lens (Larramendy North locality) that can be traced south to underlie the mammoth specimen. One anuran specimen (reported here) was recovered along with other amphibian and mammalian remains from within this lens. Because of the calibrated 14C-dated alluvial relationship, the anuran remains are accepted to be at least 13,393 years old. Based on the relative lack of alluvial wear on the anuran, other micro-vertebrate, and mammoth remains, we presume that these specimens represent local canyon inhabitants that lived within the immediate environment.

Daisy Cave, San Miguel Island.—Daisy Cave (CA-SMI-261) and its adjoining rockshelter, Cave A (CA-SMI-261A) are considered by archaeologists as a single fossil site, which is located on the northeastern coast of San Miguel Island (Fig. 1). The locality contains stratified artifact- and fossil-bearing deposits that have received numerous excavations (see overview in Erlandson et al. 1996). Renewed work in the cave in the mid-1980s and 1990s discovered stratified layers with hundreds of thousands of microvertebrate and avian remains (Guthrie 1980, 1998, 2005; Ainis and Vellanoweth 2012; Allen 2013). The chronology of the stratigraphy is well established for most of the cave with the lower levels (150–160 cm depth) reaching back to 18,670 calibrated years before present (cal yr B.P.; Beta-77070), which indicates that the locality was receiving skeletal remains before the use of the site by humans approximately 11,600 calibrated years ago (Erlandson et al. 1996).

Fossil frog remains reported here were recovered from two tests pits (TP-1, TP-2) excavated in 1986 (field notes Don Morris; NPS archive) in the middle and inner chambers of Cave A (CA-SMI-261A), areas that have received less chronological assessment. The location of TP-1 is on the stratigraphic profile of the middle chamber of Cave A (Erlandson et al. 1996, Fig. 4). The fossil sample from TP-1 was recovered from excavation layer 3B (field notes Don Morris, 1986; NPS archive), however it is not clear how this layer designation relates to the chronological strata (I-XV) established in Erlandson et al. (1996, Fig. 4). The depth of field notes layer 3B appears to be equivalent to the depth of chronological stratum XII (a distance of about 3 m apart). Radiocarbon data "suggests that the base of the [cultural] midden inside Cave A may have been deposited as much as 10,060 yr ago" (Erlandson et al. 1996: 366). A radiocarbon date from Stratum XIV is approximately 18,600 (Beta-77070) but could be recording an "old wood" issue (Erlandson et al. (1996: 369). The anuran bone from this test pit is conservatively assumed to be at least 10,060 years old based on the above discussion (earliest Holocene).

The fossil from TP-2 level 1, from the back portion in Cave A cannot be dated accurately based on stratigraphy. Based on field notes (Don Morris, 1986; NPS archive), the stratigraphy in this area of Cave A does not appear to be mixed. Level 1 sediments represent the top 5 cm of deposit and have not been radiocarbon dated. Based on discussion and data presented in Erlandson et al. (1996, Table 1), the fossil frog from this area dates less than about 3,000 years old (middle late Holocene).

Excavated sediments from both test pits were, for the most part, screened through a 3.16 mm (1/8") mesh in the field and then processed through 1.58 mm (1/16") mesh in the lab before microfossils were removed. Screened vertebrate remains displayed a mixture of white, brown, and dark-brown colored skeletal remains in all excavated strata. Due to the lack of digestive etching or mastication breakage, all microvertebrate remains are attributed to the stomach pellets produced by the barn owl (*Tyto alba*; Guthrie 2005). Other bird species, such as the burrowing owl (*Athene cunicularia*; e.g., Trulio and Higgins 2012; Wingert 2012), recovered in the cave and elsewhere on the island also produce stomach

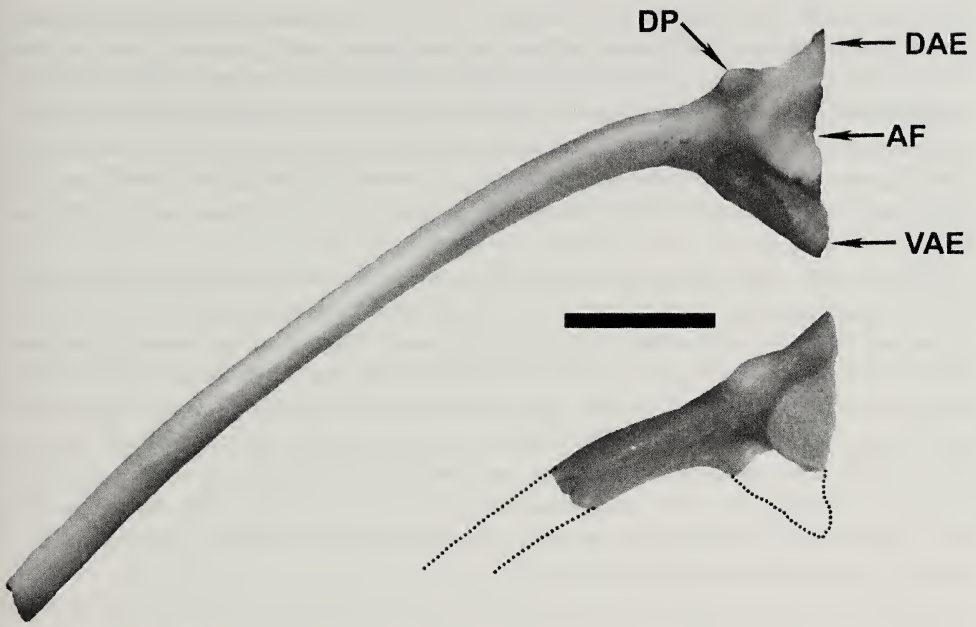

Fig. 2. Left ilia of extant *Pseudacris regilla* (top; svl = 40 mm) and fossil *Pseudacris* sp. from Santa Rosa Island, Northern Channel Islands, CA, bottom (CHIS 46774). Abbreviations: AF, acetabular fossa; DAE, dorsal acetabular expansion; DP, dorsal prominence (tubercle); VAE, ventral acetabular expansion. Scale bar equals 2 mm.

pellets and could be contributors, as well, to the bone deposits. A number of species of owls (Tytonidae, Strigidae) frequent the NCI today and likely did in the past (Collins and Jones 2015). Field studies indicate that there is only one instance of an owl pellet on one of the islands that contained an obvious transport from the continental coast (*Thomomys bottae*; PWC field notes). Studies of the food habit of eagles and barn owls from the islands have not shown that anurans or salamanders form a part of their diet today, but reptiles are occasionally recorded (Rudolph 1970; Fellers and Drost 1991; Collins et al. 2005; Erlandson et al. 2007; Collins and Latta 2009; Newsome et al. 2010, 2015). Worldwide anurans are rare in the diet of *Tyto* today (Jaksić et al. 1982).

Results and Discussion

Fossil remains.—Ilium.-A single left ilium (CHIS 46774; Fig. 2) was recovered from Larramendy North. The specimen is fragmented, being 4.8 mm in length with 50% of the ilial shaft preserved (measurements follow those in Bever 2005). No dorsal ilial crest is present. A fragment of the ventral acetabular expansion exists, indicating that the specimen originally had at least a minimal flange. The dorsal acetabular expansion is complete and pointed yet not overly prominent and is 0.8 mm in height. The acetabular fossa is 10.0 mm long and 15.0 mm in height. The tubercle on the dorsal prominence is pronounced, tall, positioned posterior to the anterior edge of the acetabular fossa, with a round, blunt apex oriented both anteriorly and laterally.

Comparison of CHIS 46774 with extant taxa includes species from around North America and not limited to just California species or with fossil species presumed to be or reported to be from the Pleistocene of the western region. The ilium is often considered

to be one of the best skeletal elements upon which to base fossil anuran identifications. Unfortunately, the morphological traits on the bone show a wide range of variation, both inter-specifically and ontogenetically. Bever (2005) did a detailed analysis of ilial characters on *Bufo* (now considered to include multiple genera). His results indicate that no distinctive morphologies in the ilium of extant *Bufo* species are known that permit a complete unambiguous species-level diagnosis. However, there are morphologies on the ilium from select anuran families that do permit some generic-level identifications and will be used here.

Although size alone is a poor character to use to make an identification, it does permit some comparative aspects that when grouped with osteological characters does allow for a certain degree of classification. Without the presence of a dorsal ilial crest on the ilium, CHIS 46774 does not belong to any member within the true frogs, Ranidae. Size ranges (using snout-vent length; svl) within extant scaphiopodids (spadefoot toad, Scaphiopodidae) *Scaphiopus* (*Sc. couchi* svl = 22–78 mm, n = 14; *Sc. holbrookii* svl = 37–61 mm, n = 8; *Sc. hurterii* svl = 50 mm) and *Spea* (*Sp. intermontana* svl = 35–53 mm, n = 6; *Sp. bombifrons* svl = 43–55 mm, n = 6; *Sp. hammondii* svl = 24–~60 mm; n = 5; *Sp. multiplicata* svl = 48–50 mm, n = 3) all have a low-rise to non-existent (juveniles) dorsal protuberance unlike what is observed on CHIS 46774.

Bufonidae is a large and complex family of true toads. All North American members used to be considered within a single genus, *Bufo*; now these have been segregated into separate genera. *Anaxyrus cognatus* (Great Plains toad svl = 61 mm) has a distinctly tall, steep-sided dorsal protuberance. The small *Anaxyrus debilis* (green toad svl = 33) has a distinct, low-rising dorsal protuberance, along with a short, lobbed ventral acetabular expansion, and a short dorsal acetabular expansion, all different than observed on CHIS 46774. *Anaxyrus microscaphus* (Arizona toad svl = 33 mm) along with *Incilius mazatlanensis* (Sinaloa toad svl = 75 mm) and the large *I. alvarius* (Colorado River toad svl = ~ 110 mm) have a prominent, steep-sided dorsal protuberance unlike CHIS 46774. Other large and small North American bufonids follow suit with those described above indicating to us that CHIS 46774 is not from Bufonidae.

CHIS 46774 is similar to a number of smaller, more delicate anurans within the families Hylidae, Microhylidae, Eleuthrodactylidae, and Craugastoridae; comparisons are made with members of these clades. *Pseudacris regilla* (Hylidae) ilia used in this study are from specimens that have a svl ranging from 32–44 mm (n = 6); also used were *P. triseriata* with svl ranging from 21–29 mm (n = 16), and *P. cadaverina* with svl of 45 mm. The ilium of *Gastrophryne* (narrow-mouth toad; Microhylidae, svl = 20–40 mm), *Eleutherodactylus* (chirping frog; previously in part within *Syrrhophus*, Eleuthrodactylidae, svl = 16–38 mm), and *Ascaphus* (tailed frog; lives today in the wet environments of the northwest of the USA; *Ascaphus*, svl = 25–51 mm) are minute, distinctly smaller than that of *Pseudacris* and the fossil. The ilium of *Ascaphus* has a large acetabulum in comparison to the acetabular expansions, and the dorsal prominence and tubercle are nearly absent (see Ritland 1955; Gardner et al. 2010), unlike the fossil presented here. The ilium of the minute *Acris* (cricket frog, Hylidae, svl = 16–32 mm; eastern USA) has a miniscule dorsal crest on the ilial shaft unlike what is observed on the fossil and *Pseudacris* (Chantell 1968a). *Craugastor* (barking frog; southern Arizona and east; Craugastoridae; previously in part *Eleutherodactylus*) is a larger frog (svl = 51–95 mm) and has distinctly small acetabular expansions and dorsal prominence as compared those found on *Pseudacris* spp. The ilium of *Smilisca* (lowland burrowing treefrog of southwestern Arizona today; another hylid once referred to as *Pternohyla*; svl = 38–63 mm) is about the size of that of many *Hyla* and has a pronounced

dorsal tubercle on a less pronounced dorsal prominence. The tubercle is knob-like, linear in shape (n = 2 in comparisons), and almost touches the acetabulum, features which are unlike those found on smaller *Pseudacris regilla* and the fossil.

Holman (2003) aptly points out that the ability to identify all species within North American Hylidae using isolated skeletal elements is surely not possible. We agree; however, there are characters on select elements, such as the ilium, that do permit a more refined level of identification than just the genus. A number of characters of the ilium have been used to identify species of both *Pseudacris* and its sister-taxon, *Hyla* (Lynch 1965, 1966; Chantell 1968b; Holman 2003). The ilium of the eastern-southeastern USA *H. cinerea* (Green treefrog) has been well-studied with regards to ontogenetic changes (Lynch 1965). The dorsal prominence enlarges through life but the tubercle, which also enlarges, never develops into a pronounced knob (Lynch 1965: Fig. 4) as observed on *Pseudacris regilla* and the fossil. *Hyla arenicolor* (Canyon treefrog) is a larger frog than *P. regilla* and it never produces the large dorsal prominence with distinctive knob tubercle of the chorus frog and fossil. A large, knob-like dorsal tubercle on *P. regilla* and the fossil are near identical; somewhat similar, yet less pronounced tubercles are found on the extinct, late Pleistocene *H. baderi* (Lynch 1965; Florida) and the extinct, late Miocene *P. nordensis* (Chantell 1964; Nebraska). Chantell (1970) found that the dorsal acetabular expansion is distinctly 'longer' on *H. arenicolor* and *P. cadaverina* (reported then as *Hyla californiae*) as compared to *P. regilla* and as seen on the fossil. In our study here using a single comparative specimen we concur with this finding.

Given the above discussion, we identify the fossil ilium as *Pseudacris* sp.: 1) it is the lowest level that skeletal morphology permits us to attempt, 2) realizing that it appears morphologically closest to *P. regilla*, and 3) yet realizing that not all species of *Pseudacris* and *Hyla* have been directly compared or are understood.

Tibiofibula.—Two tibiofibulae were recovered from Daisy Cave (SMI-261A): Test 1, Level 3B (CHIS 46773), Test 2, Level 1 (CHIS 46772). Tibiofibula CHIS 46772 is nearly complete with a length of 13.0 mm and a mid-diaphysis diameter of 0.9 mm. CHIS 46773 is nearly complete with only the proximal end absent above the crista cruris; length is 15.0 mm with a mid-diaphysis diameter of 0.8 mm. Both tibiofibulae are slightly more robust (especially at the distal end) than those observed for extant *Pseudacris regilla* (svl = 40 mm; length 16.2–19.0 mm; diameter 0.8 mm; n = 2). Overall the tibiofibulae of anurans have a generalized morphology with differences observed within some families at the generic level. Tibiofibulae within the Hylidae are typically long and slender. The NCI fossils presented here are within the morphological shape and size observed for the larger forms of *Pseudacris* (e.g., *P. regilla*) and *Hyla* (e.g., *H. arenicolor, H. chrysoscelis*) and unlike the smaller and more delicate, or distinctly long-and-slender tibiofibulae observed on, e.g., *P. triseriata*, *Acris* spp., *H. cinerea*, *H. squirella*, *H. femoralis*, to name a few. Due to the non-distinctiveness in morphology and the uncertainties mentioned above, the identification of the two tibiofibulae is cf. *Pseudacris*. A detailed study of the morphological variation among tibiofibulae should be attempted to better resolve the identification issues but is beyond the scope here.

Extant chorus frog and other Californian anurans.—Recent molecular analysis of treefrog phylogenetics produced a non-ranked clade (Arboranae) consisting of three families, including the chorus frogs in Hylidae (Duellman et al. 2016). Hylidae, as described by these authors, contains seven subfamilies with upwards of 670+ species. Results from molecular assessments vary within the family, with contrasting uses and combinations of genera and species (see discussions and details within Recuero et al. 2006; Wiens et al. 2010; Du-

ellman et al. 2016). Of importance here are the chorus frogs within the family Hylidae, a clade distributed nearly worldwide. Most are small, long-legged frogs, often with adhesive toe pads used in climbing. Eggs are deposited in water or on vegetation adjacent to water, thereby supporting their aquatic larvae, an important consideration when discussing insular sustainability.

Here we follow Stebbins and McGinnis (2012) and recognize the taxa *Pseudacris regilla* (Pacific chorus frog; sometimes referred to as *P. hypochondriaca*, Baja chorus frog, Green et al. 2013) and *P. cadaverina* (California chorus frog) as the only hylid frogs in California today. In this taxonomic scenario only *P. regilla* is thought to be indigenous on the NCI. Green et al. (2013) have *P. regilla* in the extreme north, coastal portion of California with *P. sierra* (Sierra treefrog) occurring over much of the state and *P. hypochondriaca* only in the more southern western part of the state and out on the Channel Islands. *Pseudacris regilla* (following Stebbins and McGinnis 2012) is a small frog (svl = 19–50 mm) that occurs today throughout California and north except in desert regions without perennial streams or oases. This species will coexist with *P. cadaverina* along coastal southern California. Living in a wide variety of environments, a habitat generalist, *P. regilla* can be found in the slightly brackish marshes at sea level. *Pseudacris cadaverina* is slightly larger than *P. regilla* (svl = 32–57 mm) and lives today in the Transverse and Peninsular ranges of southern California south into Baja California, Mexico, and is more closely bound to areas of freshwater than is *P. regilla* (Stebbins and McGinnis 2012).

Other hylids such as *P. triseriata* (Western chorus frog), *Hyla arenicolor* (Canyon treefrog), and *H. eximia* (Mountain treefrog) occur well to the east of western California, in Arizona, Idaho, Sonora (Mexico), and Utah. Other anurans living today in California include the spadefoot toads (*Spea*, *Scaphiopus*; Scaphiopodidae), tailed frog (*Ascaphus*; Ascaphidae), true toads (*Anaxyrus*, *Bufo*, *Incilius*; Bufonidae), and true frogs (*Lithobates*, *Rana*; Ranidae) (Stebbins 2003; Green et al. 2013).

Conclusions

The four islands of the NCI, southern California, have received many decades of work relating to natural and human history. Paleontological and zooarchaeological analyses have focused on the skeletal remains of the pygmy mammoth, birds, and micro-mammals (see previous references) in addition to paleobotanical studies including those related to fire history (Chaney and Mason 1930; Anderson et al. 2008; Kennett et al. 2008; Anderson et al. 2010; Hardiman et al. 2016;). These analyses have produced a detailed story about climatic, cultural, and environmental changes through the late Pleistocene and Holocene. Amphibians and reptiles in the fossil and subfossil record have barely received any attention due to their scant remains recognized in, or recovered from, the sedimentary record. Reptile remains (snakes and lizards) recovered from owl roost localities have received cursory presentations in a few studies centered on other taxa or cultural remains (e.g., Guthrie 1993; Allen 2013). Remains of the first fossil slender salamander (*Batrachoseps*) from NCI were recovered in 1997–1998 adjacent to a mammoth skeleton being excavated from late Pleistocene sediments on Santa Rosa Island (Mead et al. 2004); the retrieval methodology was to use 700 μm or smaller meshes to wet sieve for microfauna. This same procedure is being used now to locate additional remains from predominantly geological and paleontological localities and is producing new information about the insular herpetofauna.

Chorus frog.—The extant amphibian fauna on the NCI is depauperate (Schoenherr et al. 1999). The salamander, *Batrachoseps pacificus* is endemic on all four islands while

B. nigriventris is known only from Santa Cruz Island, but also from the adjacent coastal California (Stebbins and McGinnis 2012). Known also from the adjacent coastal California, *Pseudacris regilla* inhabits only Santa Cruz and Santa Rosa islands today. *Rana draytonii* (red-legged frog) was introduced to Santa Cruz Island in the early 1900s by ranch hands working on the island (Jennings 1988) and disappeared sometime soon after being collected in May 1919 (Sweet and Leviton 1983). The detailed analysis of sedimentary deposits from the islands is helping to assess the insular history of the amphibian fauna of the NCI.

Presented here are the fossil skeletal remains of 1) *Pseudacris* sp. from alluvial sediments with a radiocarbon date of approximately 13,393 cal yr B.P. from Santa Rosa Island and 2) cf. *Pseudacris* from Daisy Cave (CA-SMI-261A) from possibly earliest and middle late Holocene levels on San Miguel Island. At 13,000 years ago, the four islands of NCI were still connected due to lower sea levels creating the single island, Santarosae (see discussion in Reeder-Myers et al. 2015). The implication of the existence of this single-island scenario and the recovery of *Pseudacris* on San Miguel Island is that the chorus frog likely occurred over the entire Santarosae landmass, given the presence of more extensive freshwater habitat available for frogs. With rising sea levels, Santarosae began to separate into the individual islands by about 11,000 yr B.P. with Santa Cruz separating from Santa Rosa and San Miguel between about 9,900 and 9,400 yr B.P., and Santa Rosa separating from San Miguel between 9,400 and 9,100 yr B.P. (Reeder-Myers et al. 2015). One would expect the *Pseudacris* population on San Miguel Island to disappear as sea levels rose and the island shrunk in size becoming isolated from Santa Rosa Island. However, the species likely persisted on the two largest islands (Santa Rosa and Santa Cruz) due to the greater availability of suitable freshwater breeding habitat and to the larger overall size of each island and *Pseudacris* population. A question arises as to when the suitable habitat for *Pseudacris* did disappear from San Miguel Island. The specimens from Daisy Cave provide little to answer this other than to indicate that the chorus frog did once inhabit San Miguel Island where it does not today.

How and when *Pseudacris* first inhabited Santarosae (or its individual islands) is not understood. Given the geology of the islands and continent, we assume that the chorus frog colonized the insular habitat via rafting vegetation from coastal California (e.g., 'overwater waif distribution' in Savage 1967). The fossil remains of *Pseudacris* are not suitable for species identification in our view (following Bell et al. 2010). One parsimonious conclusion, however, given the current geographic distribution of the taxon, is that the insular fossils represent *P. regilla*. The previous discussion indicates that the ilium is most similar in morphological features to *P. regilla*, and does provide a reason as to why the fossil likely does not represent *P. cadaverina*, another chorus frog living along the adjacent southern California coast. But until more fossil remains of the frog are recovered and those remains are deemed useful for species-level identification, we err on the conservative side in case there was actually a different species of chorus frog on Santarosae during the Pleistocene which became extinct and has since been replaced by the extant form.

Channel Islands.—The maritime Mediterranean climate of moist winters and warm, dry summers of the NCI is largely controlled by the oceanic currents that sweep by southern California. Based on the bathymetry, this scenario was likely similar during the late Pleistocene glacial regime. San Miguel, Santa Rosa, and the western end of Santa Cruz islands are almost constantly bathed by strong northwesterly winds, which then create greater precipitation on the western and northern sides of the highlands of each island (or most of Santarosae in the late Pleistocene) (Junak et al. 1995; Schoenherr et al. 1999). Each island

today has its own peculiarities in geology, island size, mountain elevations, temperature, and precipitation. Santa Cruz Island is the largest of the islands, has two distinct mountains ridges with a Central Valley in the middle, has two distinct geological histories, has abundant groundwater with numerous springs and seeps, and is likely the most studied of the islands' natural history. Today the local vegetation on the islands is dominated by grassland and shrubland species along with patchy woodlands and chaparrals (see overview in Junak et al. 1995 and Schoenherr et al. 1999). Clearly the presence of humans on the islands, especially since the ranching enterprises of the 19th century, has drastically altered the pre-human environments. Details about the vegetation history of the NCI is still in its infancy of being understood.

Placing the fossil chorus frog into a reconstructed habitat is not straightforward due to the complexities of the plant fossil data. On Santa Cruz Island, Chaney and Mason (1930) recovered macrobotanical remains in Cañada de los Sauces that record the existence of a late Pleistocene coniferous plant community including *Pseudotsuga* (Douglas fir), *Cupressus* (cypress), and *Pinus* (pine) radiocarbon dating 16,600 ± 270 cal yr B.P. (Anderson et al. 2008). A coastal salt marsh (Abalone Rocks Marsh; Cole and Liu 1994) and a small ephemeral wetland (Soledad Pond, island central) on Santa Rosa Island were studied and provide community reconstructions. At 11,900 cal. yr B.P. Santa Rosa Island had a variety of communities including pine forests, coastal sage scrub, and grasslands in the central portion of the island; coastal records indicate at least some coniferous forest occurrence. The transition from the late Pleistocene to Holocene was a period of major environmental change (see overview in Anderson et al. 2010). The record from the central-island pond suggests increasingly drier conditions during the early Holocene; the pond had dried more than once during this time (approximately 9,150 to 6,800 cal yr B.P.). Arlington Canyon on the island records a pine woodland during the late Pleistocene (Kennett et al. 2008). Plant records from Daisy Cave, San Miguel Island provide a similar late Pleistocene plant community reconstruction (see overview in Erlandson et al. 1996; Anderson et al. 2010).

The reconstructed late Pleistocene flora for Santarosae during the late glacial climate includes forest and woodland habitats with a diverse understory, as is characteristic of modern northwest coastal California. All of the above implies that habitat reconstruction of the late Pleistocene through Holocene plant community structure was somewhat complex and may have changed quickly at the end of the last glacial maximum. As the plant communities transformed their mosaic structures and responded to both climate and sea level changes, so too would the herpetofaunal species, especially the moisture-dependent amphibians. With the above frog fossils now known from Santa Rosa Island (Larramendy North) and San Miguel Island (Daisy Cave), it is understood that the chorus frog, *Pseudacris* sp., lived on glacial-age Santarosae Island, but it is not understood when its distribution was reduced to just the two largest islands, Santa Rosa and Santa Cruz.

If the fossils do represent *Pseudacris regilla*, and the late Pleistocene species had the same "habitat generalist" requirements and ability to live in "slightly brackish cattail marshes at sea level" as the living form (Stebbins and McGinnis 2012:181), then the climate changes at the end of the Pleistocene with transformations in the vegetation mosaic may not have had much direct impact on the frog. As long as some sort of vegetation occurred along brackish marshes, ponds, and streams, along with the sustainability of the seeps and springs, the frog should have evaded any major population crisis. However, the rise in sea level beginning around 11,000 years ago may have caused the critical reduction in distribution. At some point, *Pseudacris* found Anacapa and San Miguel, the smallest islands, uninhabitable. Whether this is due to lack of ponding water, seeps, and springs, or habitat destruction

due to fires is not understood at this time. The possibility of changes in distribution and density of the frog could have occurred during the known dry period 9,159–6,800 cal yr B.P., as recorded at Soledad Pond, Santa Rosa, which recorded distinct dry-pond episodes (Anderson et al. 2010). Future paleontological research on the NCI should examine both rock shelter deposits (raptor roosts) and open-air alluvial (geological) localities on all four islands with the methodology to wet sieve screen washing all sediments through 0.5 mm (500 μm) screens, sort retained matrix with the aid of a microscope, and develop an accurate site-specific chronology.

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Aspects of the Life Histories of Pinkrose Rockfish (*Sebastes simulator*) and Swordspine Rockfish (*Sebastes ensifer*) with Notes on the Subgenus *Sebastomus*

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The rockfishes, genus *Sebastes*, form an extremely speciose group that often dominates the fish assemblages of California reefs between depths of 30 and 300 m (Love et al. 2002). The genus is divided into a number of subgenera (estimated at between 13 and 15, Hyde and Vetter 2007) among which the subgenus *Sebastomus* is particularly well characterized by congruencies in both morphology and genetics (Chen 1971; Rochas-Olivares et al. 1999; Hyde and Vetter 2007). In general, species in this subgenus are relatively small (to a maximum of 56 cm total length) (Table 1) and all are benthic or epibenthic (Love 2011). In addition, with the exception of *Sebastes helvomaculatus*, all of the North American species are relatively warm-water, and most are rare or absent from waters north of central California (Table 1).

The basic biology and ecology of most of the *Sebastomus* living in the northeastern Pacific (i.e., with ranges extending at least into California waters) have been fairly well documented (summarized in Love et al. 2002; Love 2011; Fields 2016). The main exception was *Sebastes simulator*, the pinkrose rockfish, and to a lesser extent, *Sebastes ensifer*, the swordspine rockfish, whose life histories, were poorly understood. In this paper, we report on a number of aspects on the biology of *S. simulator*, provide supplementary data on the biology of *Sebastes ensifer*, and update basic information on all species in the subgenus *Sebastomus*. We collected specimens by hook-and-line from southern California waters (primarily from the northern Channel Islands), immediately placed them on ice aboard a research vessel, and then froze them in the lab for later examination. All specimens were measured [standard (SL), fork (FL), and total (TL) length] to the nearest millimeter and most were weighed (to the nearest 0.1 g). All lengths are reported as TL.

We used sagittal otoliths for age determinations; these were removed and stored dry in coin envelopes. For age determinations, each otolith was glued to a wooden block, placed on a Bueller Isomet low-speed saw and a 0.05-cm wafer was cut from it, using two diamond-edge blades separated by a stainless-steel shim. Before reading, the wafers were slightly burned over an alcohol lamp. The wafers were then placed in a water-filled, black-bottomed watch glass and examined under a dissecting microscope. All wafers were read twice by M. Love. When reading did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age. We judged that the otoliths of about 5% of the specimens were unreadable due to poorly developed annuli.

Lengths at ages were estimated by direct observation of otolith annuli and by using the von Bertalanffy growth model:

$$L_t = L_\infty [1 - \exp - k (t - t_0)],$$

Where L_t = length at time r;

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Table 1. Species of the subgenus *Sebastomus* including maximum lengths, geographic ranges, and depth ranges. LACM = Los Angeles County Museum of Natural History; SIO = Scripps Institution of Oceanography Marine Invertebrate Collection; CAS = California Academy of Science; RACE = Resource Assessment and Conservation Engineering Division, NOAA; SAIAB = South African Institute for Aquatic Biodiversity; SCCWRP = Southern California Coastal Water Research Project.

Sebastes capensis (Gmelin, 1789). **Cape Redfish**. 40 cm (15.7 in) TL (SAIAB 18249). Argentina, Falkland Islands, Trista de Cunha Island, and southern Africa (Venurus 2013). 4–223 m (13–731 ft) (min.: SAIAB 18242; max.: SAIAB 74972). Historically, this species has been confused with *S. oculatus*. Based on recent research (Venurus 2013), fish from at least Peru and Chile, once thought to be *S. capensis*, are now assumed to be *S. oculatus*. Therefore, length and depth records of "*S. capensis*" from the southeastern Pacific are not valid. In addition, *S. capensis* and *S. oculatus* co-occur off Argentina and there has likely been confusion in identifying the two species off that coast. Thus, the size and depth data we present are taken from museum records of individuals living in areas where only *S. capensis* is known to exist.

Sebastes chlorostictus (Jordan & Gilbert, 1880). **Greenspotted Rockfish**. 53.4 cm (21 in) FL (D. Pearson, pers. comm. to M. Love). Vancouver Island (49°04'N, 126°50'W) (Canada Department of Fisheries and Oceans, unpubl. data) to at least Isla Cedros (28°22.62'N, 115°17.46'W), central Baja California (collected by M. L.) or perhaps to southern Baja California (25°32'N, 113°04'W; Snytko 1986) but without documentation. At depths of 30–379 m (98–1,243 ft) (min.: M. Love, unpubl. data; max.: RACE).

Sebastes constellatus (Jordan & Gilbert, 1880). **Starry Rockfish**. To 46 cm (18 in) TL (Phillips 1957). Off the mouth of the Russian River, northern California (CAS 26375) to off Todos Santos (23°24'N, 110°14'W), southern Baja California (J. Snow, pers. comm. to M. Love). Tentatively identified from photographs taken at Rocas Alijos (about 25°N, 115°45'W; R.N. Lea, pers. comm. to M. Love). At depths of 15–274 m (50–900 ft) (min.: D. Jehl, pers. comm. to M. Love; max.: Miller and Lea 1972).

Sebastes ensifer Chen, 1971. **Swordspine Rockfish**. To 30.5 cm (12 in) TL (Miller and Lea 1972). San Francisco, northern California (Miller and Lea 1972) to Banco Ranger (28°25'N, 115°32'W), central Baja California (Chen 1971). At depths of 50–433 m (164–1,420 ft) (min.: M. Love, unpubl. data; max.: Miller and Lea 1972).

Sebastes eos (Eigenmann & Eigenmann, 1890). **Pink Rockfish**. To 56 cm (22 in) TL (Phillips 1957). Central Oregon (44°33'N; RACE) to southern Baja California (27°01.2'N, 114°16.2'W) (SIO 65-203) or perhaps to 25°24'N, 113°01'W (Snytko 1986), but without documentation, and Isla Guadalupe, central Baja California (Love et al. 2002). At depths of 45–366 m (150–1,200 ft) (min.: Allen et al. 2002[1]; max.: Miller and Lea 1972).

Sebastes exsul Chen, 1971. **Gulf Rockfish**. To 31 cm (12.1 in) (Love et al. 2002). Gulf of California in the vicinity of Bahia de los Angeles (Love et al. 2002). At depths of 110–213 m (363–699 ft) (min.: Love et al. 2002; max.: SIO 06-266).

Sebastes helvomaculatus Ayres, 1859. **Rosethorn Rockfish**. To 43 cm (16.9 in) TL (Yamanaka 2005). Western Gulf of Alaska east of Sitkinak Island (Mecklenburg et al. 2002) to at least about U.S.-Mexican border (32°26.1'N, 119°06.6'W) (SIO 64-988) or perhaps to Banco Ranger (28°33'N, 115°25'W), central Baja California (Snytko 1986) but without documentation. At depths of 16–1,145 m (52–3,756 ft) (min.: Canada Department of Fisheries and Oceans, unpubl. data; max.: Ramsey et al. 2002[2]).

Sebastes lentiginosus Chen, 1971. **Freckled Rockfish**. To about 23 cm (9 in) TL (Miller and Lea 1972). Point Conception, central California (34°36'N; RACE) to southern Baja California (25°37'N, 113°24'W) (LACM 42178.004). At depths of 22–168 m (73–551 ft) (min.: M. L., unpubl. data; max.: SIO 48-196), reported without documentation to 290 m (951 ft) (Snytko 1986).

Sebastes notius Chen, 1971. **Guadalupe Rockfish** or Southern Rockfish. To 21.9 cm (8.6 in) SL (Chen 1971). This species has been collected at two sites: Isla Guadalupe (29°N; Chen 1971), central Baja California and in the vicinity of Banco del Tio Sam (Uncle Sam Bank; 25°35'N), southern Baja California (Rocha-Olivares 1998). At depths of 165–250 m (541–820 ft; Chen 1971).

Sebastes oculatus Valenciennes, 1833 (in Cuvier and Valenciennes, 1833). **Patagonian Rockfish** or Patagonian Redfish. 40.8 cm (16 in) TL (Venerus et al. 2016). Peru, Chile, Argentina, and Falkland Islands (Venurus et al. 2013). At least 30–271 m (98–899 ft) and perhaps to 665 m (2,181 ft) (Venerus et al. 2013). Light and dark color morphotypes, perhaps incipient species, live off Argentina (Venurus et al. 2013).

Table 1. Continued.

Sebastes rosaceus Girard, 1854. **Rosy Rockfish**. To 36 cm (14 in) TL (Eschmeyer and Herald 1983). Cobb Seamount (46°44'N, 130°47'W) (Oregon State Ichthyology Collection 15632) to Bahia Tortugas (27°30'N, 114°50'W), southern Baja California (Phillips 1957). A report from the Strait of Juan de Fuca, Washington (Echeverria and Love 2002) is undocumented. At depths of 7–328 m (24–1,076 ft) (min.: SCCWRP; max.: Bradburn et al. 2011).

Sebastes rosenblatti Chen, 1971. **Greenblotched Rockfish**. To 54 cm (21.3 in) TL (Love et al. 1990). Point Delgada, northern California (40°04'N; RACE) to Banco Ranger, central Baja California (Chen 1971). At depths of 55–491 m (180–1,610 ft) (min.: M. Love, unpubl. data; max.: Wilkins et al. 1998[3]).

Sebastes simulator Chen, 1971. **Pinkrose Rockfish**. Largest documented individual 34.5 cm (13.6 in) TL (SIO 79-73); one undocumented record at 42.1 cm (16.4 in) TL (León-Castro et al. 1993). Carmel Submarine Canyon, central California (R. N. Lea, pers. comm. to M. Love) or perhaps to Eureka, northern California (D. Pearson, pers. comm. to M. Love) to Punta Colnett (30°53'N, 116°30'W), northern Baja California (M. Love, unpubl. data) and Isla Guadalupe, central Baja California (León-Castro et al. 1993). At depths of 99–450 m (325–1,476 ft) (min.: Eschmeyer and Herald 1983; max.: Chen 1971).

Sebastes spinorbis Chen, 1975. **Spiny-eye Rockfish**. To 34.4 cm (13.4 in) (Love et al. 2002). Gulf of California in the vicinity of Bahia de los Angeles (Love et al. 2002). 130–213 m (429–700 ft) (min.: Love et al. 2002; max.: SIO 06-266).

Sebastes umbrosus (Jordan & Gilbert, 1882). **Honeycomb Rockfish**. To 28.5 cm (11.2 in) TL (M. Love, unpubl. data). Point Pinos, central California (Miller and Lea 1972) to Rocas Alijos (24°57'N, 15°44'W), southern Baja California (LACM 37658.002). At depths of 18–270 m (60–891 ft) (min.: M. Love, unpubl. data; max.: León-Castro 1993).

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L_∞ = theoretical maximum length;
K = slope of curve expressing the rate of approach to L; and
T_0 = theoretical age at which $L_t = 0$

The relationships between total length and weight fit the relationship $W = aL^b$, where W = weight in grams and L = total length in centimeters, and *a* and *b* are constants. The values of *a* and *b* were determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares. The resulting relationships were compared using an F–test. To test whether differences between genders (if any) were an artifact caused by the larger female gonads, we subtracted gonad weight from body weight, generated the length-weight relationships for each gender and again tested these between genders.

We computed condition factor (a measure of fat storage) as

$$100 \times \left[(W - GW)/L^3\right]$$

Where W – body weight (g), GW = gonad weight (g), and L – total length (cm) of mature rockfishes. Condition factor was computed using body weight with gonad weight

subtracted, so as to minimize the effects of seasonal changes in gonad size. We compared these values between seasons (reproductive and nonreproductive) within sexes and between sexes, using the Mann-Whitney U-Test (Love et al. 1990).

We determined female reproductive stages macroscopically, characterizing the ovaries into five stages (Love et al. 2002): maturing (vitellogenesis), uneyed (fertilized), eyed, spent, and resting (transitional). Within the rockfishes, it is difficult to distinguish between prereproductive and mature-resting stage females during the nonreproductive season, as at both stages females exhibit small, light-colored ovaries (Love et al. 1990; Love et al. 2002). For this reason, our analyses of age and size at first maturity only included individuals from the reproductive season. A gonadosomatic index (GSI) was calculated for female *S. simulator* (this had previously been reported for *S. ensifer* in Love et al. 1990) using the formula:

$$GSI = (GW/BW) \times 100$$

Where GW = gonad weight and BW = total body weight.

We determined egg production by counting subsamples of unfertilized eggs, referable to "gonad stage 3" in Wyllie Echeverria (1987) or "vitellogenesis" in Love et al. (2002). We used only those females taken both 1) early enough in the reproductive season that no eye larvae were observed in ovaries and 2) late enough that eggs would be large and easily counted. In the lab, eggs were incised from the ovarian membrane and place in Gilson's solution (Love et al. 1990) for about one month or until the eggs came loose from the ovarian tissue. Before counting, the ovaries were repeatedly washed and the egg masses broken up to remove remaining connective tissue. The eggs were weighed, subsamples taken, and these were weighed. Eggs in each subsample were counted and the mean number per weight calculated for each subsample. Egg production was estimated by the calculation:

$$F = (TW \times SN)/SW$$

Where F = fecundity, TW = total weight of gonads, SN = mean subsample of egg number, and SW = subsample weight.

Stomach contents were sorted taxonomically into six food item categories (copepods, crabs, euphausiids, fishes, salps, and crustacean pieces) and the volume of each category was measured by liquid displacement and presented through the Index of Relative Importance (Pinkas et al. 1971). We collected 181 *S. simulator* between 1995–2014 and 229 *S. ensifer* between 2000–2012; most individuals of both species were collected from 2007–2013. Length conversion factors between standard (SL), fork (FL), and total lengths (TL) for both species are shown in Table 2.

We aged *S. simulator* between the lengths of 10.1 and 28.1 cm. Male *S. simulator* live to at least 39 years and females to at least 32 years (Table 3). Males may grow somewhat larger than females (Fig. 1). The von Bertalanffy equation fits the male growth pattern well; however, it does not accurately predict female growth (Table 3, Fig. 1). This is likely because we aged too few young females. We aged *S. ensifer* between the lengths of 11.1 and 23.0 cm. The maximum life span of male and female *S. ensifer* may be similar as the oldest female was 38 years old and the oldest male was 37 years old (Table 3). We saw no evidence of gender-based differences in maximum length. For *S. ensifer*, the von Bertalanffy equation appeared to adequately fit the growth patterns of both genders (Table 3, Fig. 1) and, based on k values, growth rates were similar. We both measured and weighed a total of 77 males and 50 females of *S. simulator*. The overall length-weight relationship was $W = 0.004828TL^{3.33123}$; females were significantly heavier at length ($W = 0.004117TL^{3.39021}$) than males ($W = 0.003196TL^{3.45416}$) ($F = 4.2992$, $P = 0.05$). However, when gonad weight

Table 2. Conversions between standard, fork, and total lengths for *Sebastes simulator* and *S. ensifer*.

Sebastes simulator							
Dependent variable	Independent variable	n	Intercept a	Coefficient b	R^2	F	Significance
FL	SL	115	1.324	1.133	0.9817	6,119	<0.001
TL	SL	115	1.424	1.152	0.9810	5,827	<0.001
SL	FL	115	-0.788	0.866	0.9817	6,119	<0.001
TL	FL	115	0.141	1.013	0.9937	18,090	<0.001
SL	TL	115	-0.835	0.851	0.9810	5,827	<0.001
FL	TL	115	0.009	0.980	0.9937	18,090	<0.001
Sebastes ensifer							
Dependent variable	Independent variable	n	Intercept a	Coefficient b	R^2	F	Significance
FL	SL	171	0.846	1.127	0.9706	7825	<0.001
TL	SL	173	0.879	1.160	0.9871	13,210	<0.001
SL	FL	171	-0.393	0.868	0.9706	7,825	<0.001
TL	FL	171	0.278	1.015	0.9896	16,120	<0.001
SL	TL	173	-0.540	0.850	0.9871	13,210	<0.001
FL	TL	171	-0.073	0.974	0.9896	16,120	<0.001

was subtracted from body weight, there was no significant difference in the length-weight relationship ($F = 0.4929$). Length-weight relationships for *S. ensifer* are given in Love et al. (1990). For *S. simulator* we found significant within-gender differences in condition factor between seasons (Table 4). In both males and females, condition factor was slightly higher during the June–November season. Condition factors for both male and female *S. ensifer* are given in Love et al. (1990).

A few female *S. simulator* were mature at 14 cm, 50% were mature at about 17 cm, and all were mature at 18 cm (Fig. 2). Males tended to mature at a slightly larger size, a few at 17 cm, 50% at about 17 cm, and all at 23 cm. A lack of substantial numbers of young fishes made it difficult to estimate first and 50% maturity ages. However, it would appear that a few fish mature at about 8–9 years old, 50% of both males and females are mature at about 10–12 years old, and most are mature by 15–17 years old (Fig. 3). *Sebastes ensifer* maturation rates were similar, with a few females mature at 12 cm, 50% at about 15 cm, and all mature at 24 cm (Fig. 3). Similarly, a few male *S. ensifer* were mature at 12 cm, 50% at about 16 cm, and all were mature at 23 cm. Among females, this corresponded to a few fish maturing at as young as perhaps 5 years old, 50% at about 8–10 years old and all being mature at 16 years old. Maturation ages for males were similar as a few were mature at 6 years, 50% were mature at about 10 years, and all were mature in their mid-20s. For both

Table 3. Parameters of the von Bertalanffy equation for *Sebastes simulator* and *Sebastes ensifer* from southern California.

Species	Sex	L_∞	SE	K	SE	t_0	SE	Maximum observed age (yr)
simulator	female	42.612	6.332	0.026	0.008	-8.092	1.757	32
	male	27.396	0.260	0.094	0.004	0.108	0.297	39
ensifer	female	22.098	0.304	0.120	0.010	-1.674	0.574	38
	male	20.492	0.258	0.126	0.011	-2.171	0.616	37

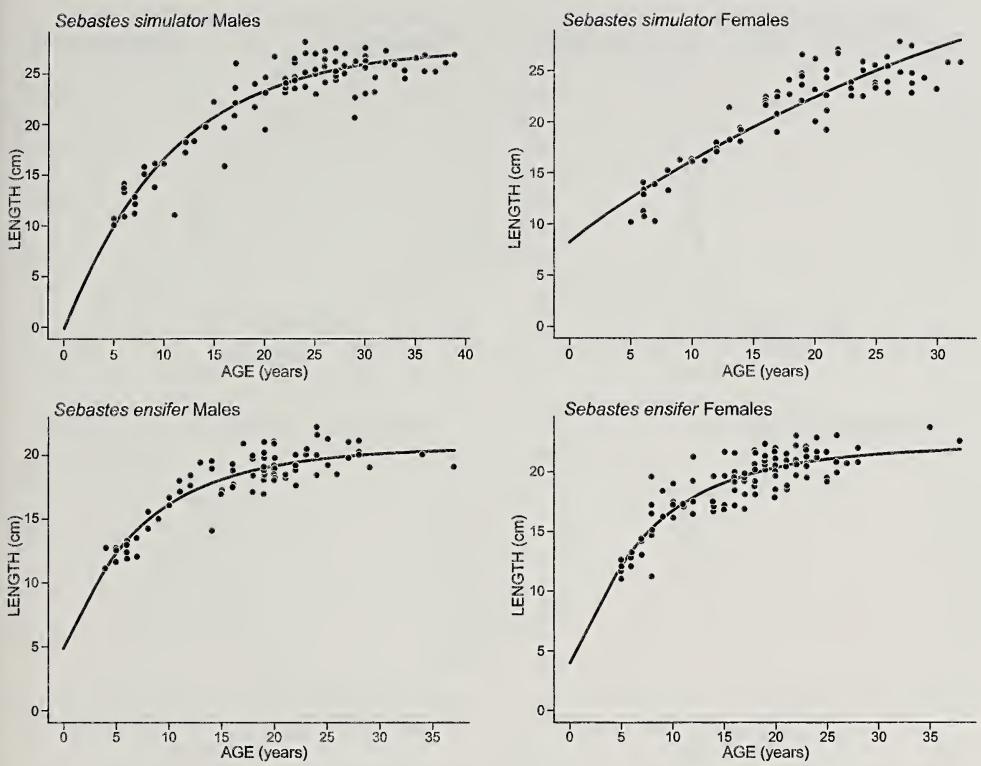

Fig. 1. Von Bertalanffy growth curves of female and male *S. simulator* and *S. ensifer*, including direct observation data points.

species, we note that assessing whether males were mature was, in a number of instances, particularly problematic.

Both *S. simulator* and *S. ensifer* released larvae between at least January and July (Table 5). It is likely that parturition for both species peaks in late winter and early spring. We note that the parturition season for *S. simulator* might extend further into the summer, but we were unable to capture specimens in August. The gonadosomatic indices for *S. simulator* reflect this pattern with maximum values peaking in February and March (Fig. 4).

Table 4. Condition factors of *S. simulator* from the southern California Bight. Significant differences are marked with an asterisk. N = number of individuals samples, K = Fulton's condition factor, U = output of the Mann-Whitney U test, and P = probability.

	N	K	U	*P*
Males				
December–May	54	1.34	232	<0.0001*
June–November	23	1.46		
Females				
December–May	32	1.32	109	0.0002*
June–November	18	1.44		
All Seasons				
Males	77	1.38	1,683	0.2334

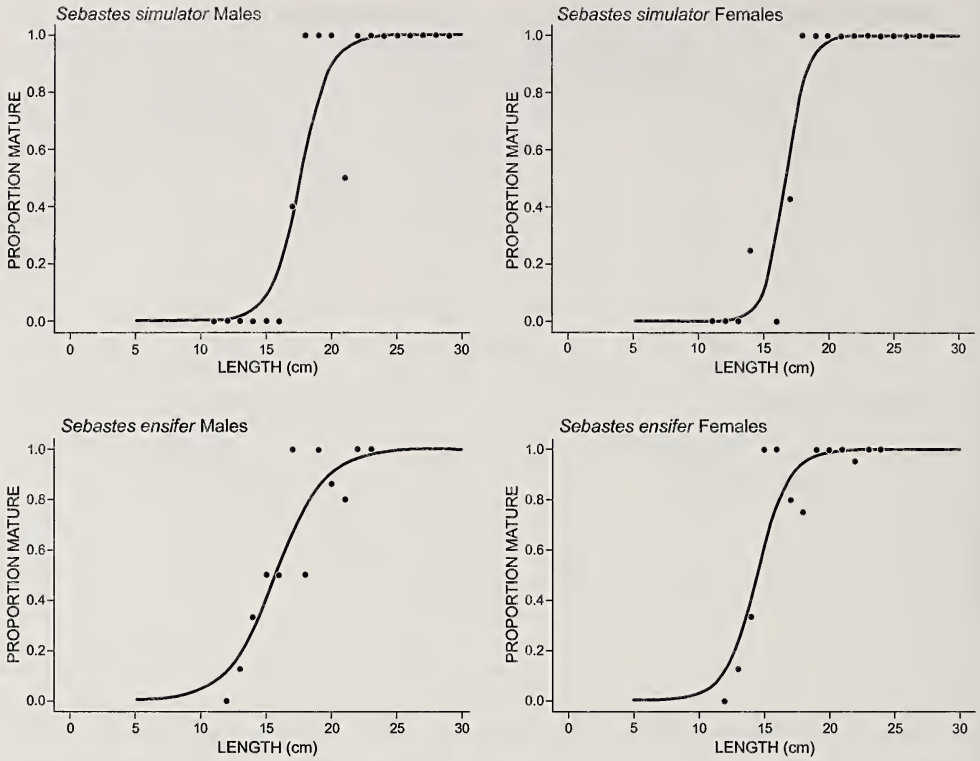

Fig. 2. Predicted proportion of mature female and male *S. simulator* and *S. ensifer* at length (solid lines) and observed proportion mature (by 1 cm length bins) (circles).

Gonadosomatic indices for S. *ensifer* are found in Love et al. (1990). *Sebastes simulator* females produced between 9,980 and 68,995 eggs within a season. Maximum egg production of *S. ensifer* was somewhat lower, ranging from 10,042 and 38,900. For both species, the relationship between length and egg production assumed a power function (Fig. 5). We saw no evidence of multiple brooding, where a female releases larvae two or more times per season. In previous research, we did observe multiple brooding in *S. ensifer* (Love et al. 1990). We found that *S. simulator* preyed primarily on benthic-oriented prey; crabs dominated their diets. By comparison, *S. ensifer* preyed mostly on water column prey, primarily euphausiids and copepods (Fig. 6).

In the northeast Pacific, growth rates among rockfish species are variable. At the extremes, some species grow quite slowly (K = 0.03, *S. borealis*; K = 0.04, *S. ruberrimus* and *S. rufus*) and some, primarily dwarf, species grow considerably faster (i.e., K = 0.5 *S. semicinctus*, *S. emphaeus*) (summarized in Love 2011). At least male *S. simulator* and both genders of *S. ensifer* grow at rates mid-range between these two extremes.

There were no previous growth rate studies of *S. simulator*. However, Chen (1971) presented an age-length relationship for *S. ensifer* (genders combined) (Fig. 7) based on reading whole otoliths as opposed to the sectioned ones we utilized. Previous research with rockfishes has shown that ageing younger individuals using whole otoliths is reasonably accurate. In older fish, however, using whole otoliths often tends to underestimate age at

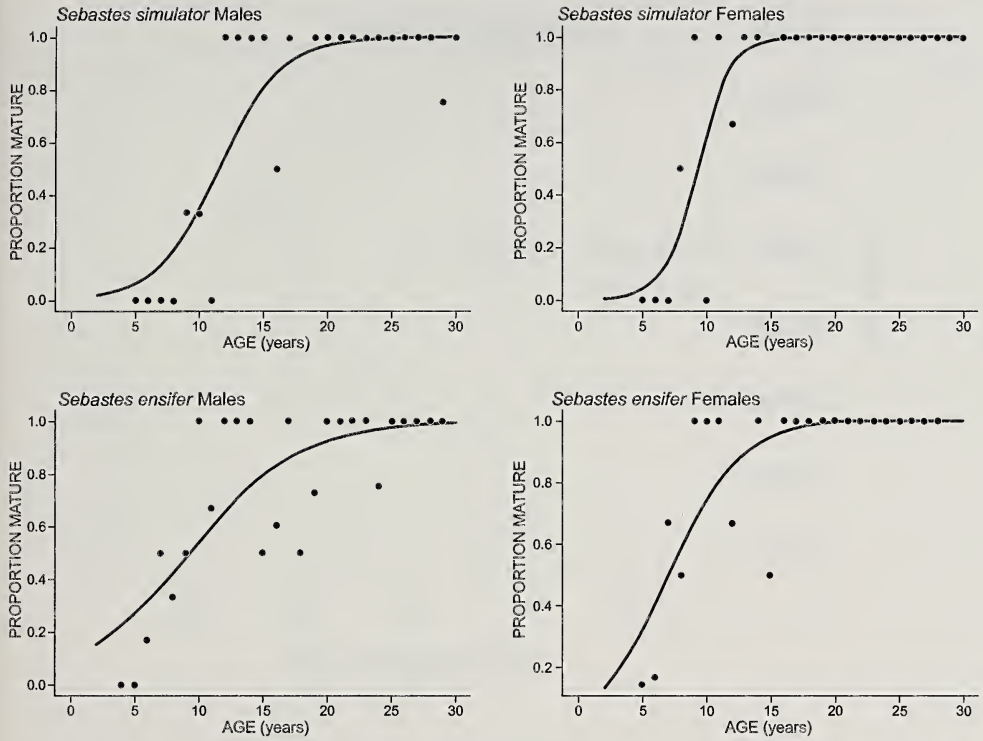

Fig. 3. Predicted proportion of mature female and male *S. simulator* and *S. ensifer* at age (solid lines) and observed proportion mature (by 1 cm length bins) (circles).

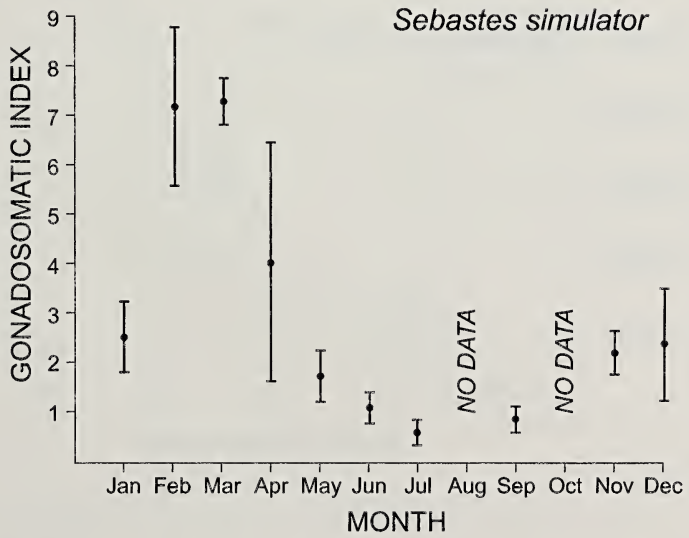

Fig. 4. Seasonal changes in the gonadosomatic indices of female *Sebastes simulator*.

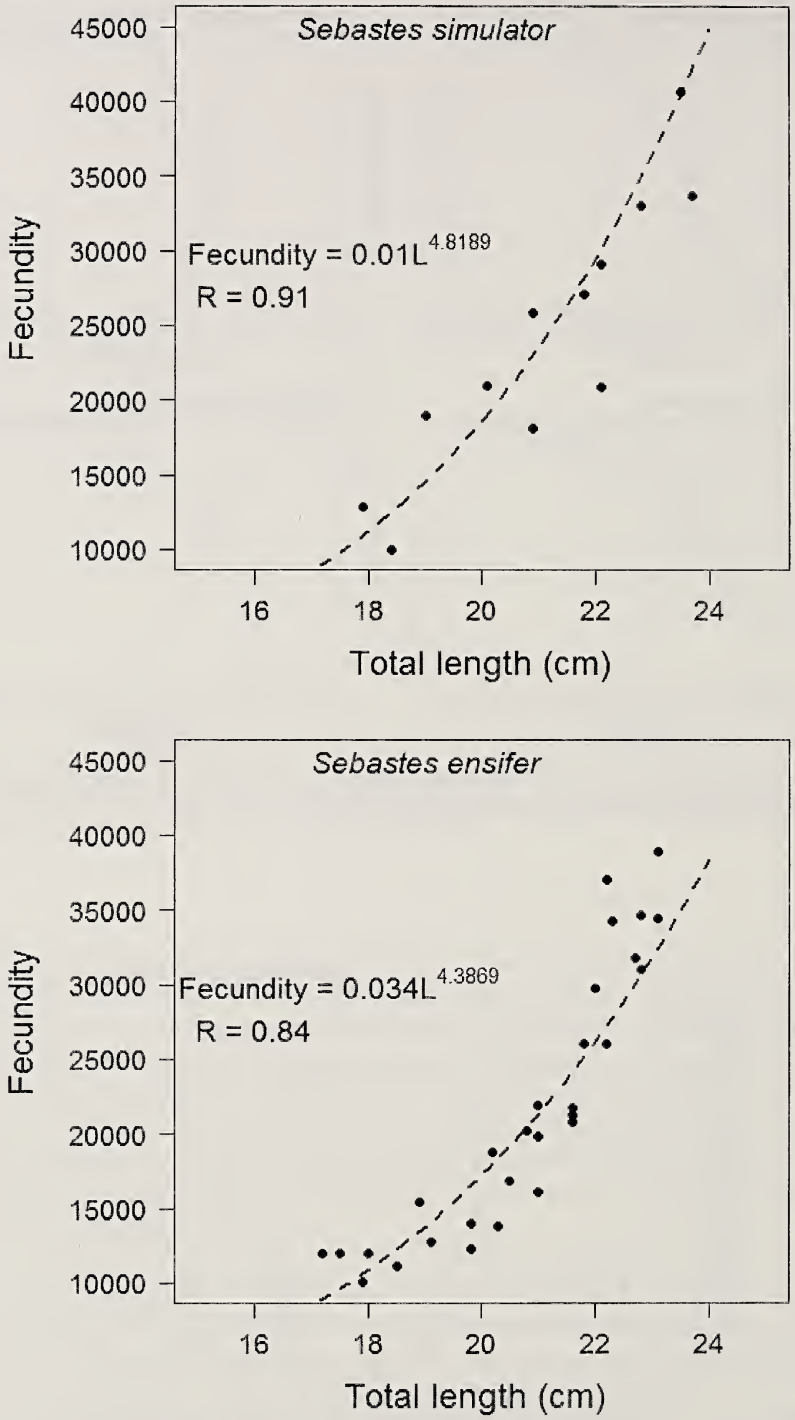

Fig. 5. Fecundity patterns of *Sebastes simulator* and *S. ensifer*.

Table 5. Reproductive stages, by month, of female *Sebastes simulator* and *Sebastes ensifer*.

Sebastes simulator	Resting	Maturing	Uneyed	Eyed	Spent
Month					
January	1	5	1	3	2
February	5	2	2		
March	6	4			
April	2	2	1	2	
May	4	5	3		
June	3	1	4	5	2
July	5	1	2	1	
August	No Data				
September	8				
October	No Data				
November	2	7			
December	8	1			
Sebastes ensifer					
January	7	2	1		
February	8	6	6	2	
March	7	8	3	5	
April	1	2	4	6	
May	6	1	1	1	
June	7	1			
July	1	1			
August	5				
September	6				
October	No Data				
November	2	6			
December	3	1			

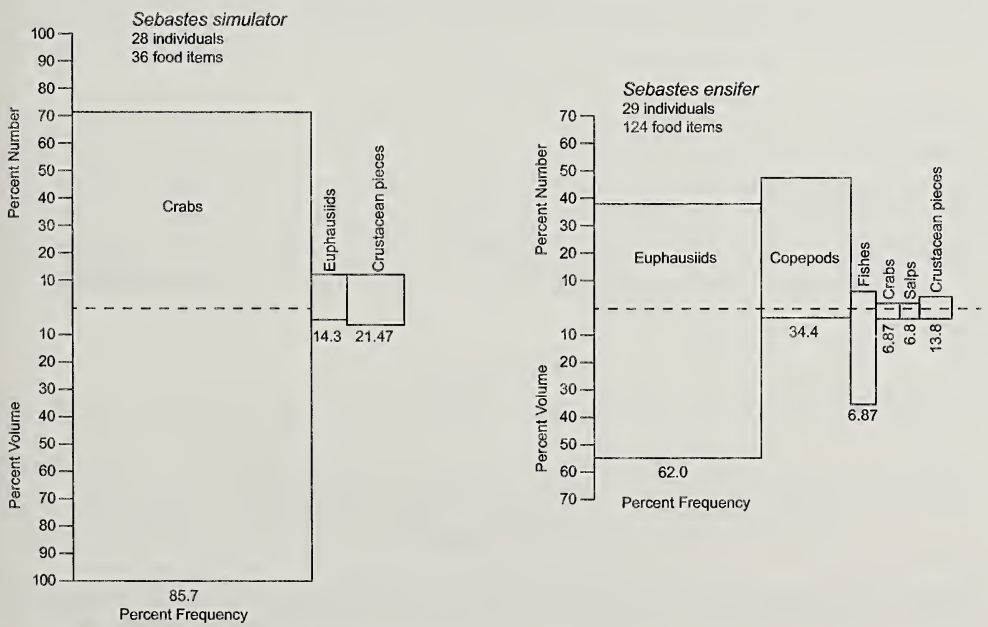

Fig. 6. Index of Relative Importance of food items eaten by *Sebastes simulator* and *S. ensifer*.

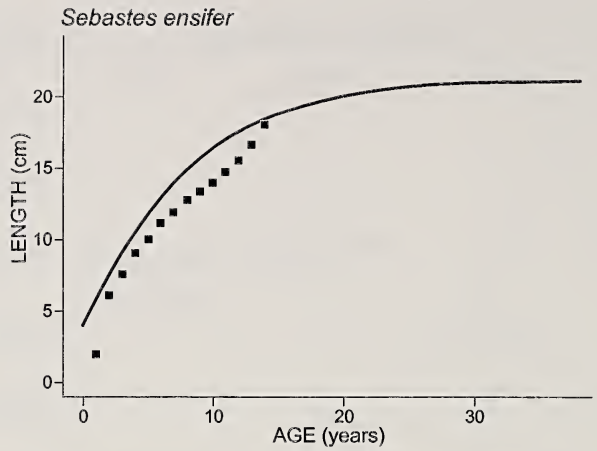

Fig. 7. A comparison of the age-length relationship of *S. ensifer* (both genders combined) between data from this paper (solid line representing von Bertalanffy growth equation) and data from Chen (1971) (squares).

length [i.e., *S. alutus* (Beamish 1979); *S. rosaceus* in Lea et al. (1999) compared to Fields (2016)].

The subgenus *Sebastomus* is of relatively recent origin having evolved around 2.5 million years ago (Hyde and Vetter 2007) and it is interesting to note that a number of life history traits seem to have been retained among the various species. For instance, with one exception, throughout the *Sebastomus* of the northeast Pacific and Gulf of California, the maximum age a species attains tends to be correlated with that species' maximum size (data from Love et al. 2002; Yamanaka et al. 2005; Benet et al. 2009; Love 2011; Fields 2016, and current data) (Fig. 8). *Sebastes helvomaculatus* is an exception as, despite its small maximum size, the species lives to at least 87 years, far longer than even its much

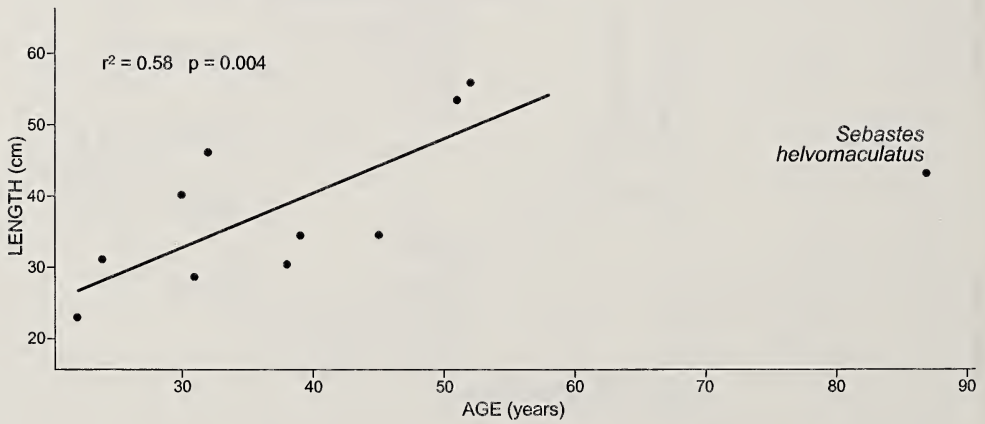

Fig. 8. The relationship between maximum length and maximum age in the subgenus *Sebastomus*. The relationship between the two variables was derived from an analysis of all species for which data were available (*S. chlorostictus*, *S. constellatus*, *S. ensifer*, *S. exsul*, *S. lentiginosus*, *S. rosaceus*, *S. rosenblatti*, S. *simulator*, *S. spinorbis*, and *S. umbrosus*) except for *S. helvomaculatus*.

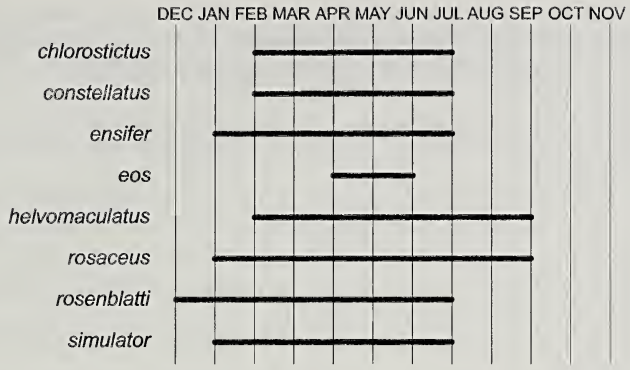

Fig. 9. Parturition season of the members of the rockfish subgenus *Sebastomus* living in the northeast Pacific.

larger congeners. *Sebastes helvomaculatus* is the only northern member (as defined by Love et al. 2002) of the subgenus. Love et al. (2002) noted that, almost without exception, within the northeastern Pacific rockfishes the more northerly species tend to live longer than congeners more typical of southerly waters. Parturition seasons are remarkably similar within the northeastern Pacific *Sebastomus* (these seasons are unknown in species endemic to the outer coast of Baja California, Gulf of California, or southern Hemisphere) (Fig. 9). Perhaps without exception (note that data on *S. eos* is very limited), the parturition season is long, commencing during the winter (between December and February) and extending well into the summer and perhaps into the early fall. Compared to other northeastern Pacific rockfishes, these seasons are relatively long (Love et al. 1990, 2002; Love 2011). Among subgenera, only members of the subgenus *Sebastodes* (i.e., *S. goodei*, *S. jordani*, and *S. paucispinis*) release larvae over as extended a period (Love et al. 1990, Love 2011).

Acknowledgements

We thank Bill Lenarz for providing some of the life history analyses. Brian Sidlaukas identified a *Sebastes rosaceus* from the Oregon State Fish Collection for us. This research was supported by the National Aeronautics and Space Administration Biodiversity and Ecological Forecasting program (NASA Grant NNX14AR62A), the Bureau of Ocean and Energy Management Ecosystem Studies program (BOEM award MC15AC00006) and NOAA in support of the Santa Barbara Channel Biodiversity Observation Network.

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Spots on Sides of Giant Sea Bass (*Stereolepis gigas* Ayres, 1859) are Likely Unique to Each Individual

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The giant sea bass (*Sterolepis gigas* Ayres, 1859; hereafter GSB) is a large and presumably keystone nearshore reef species found from California, USA to southern Mexico, including the Gulf of California. Giant sea bass were severely overfished in the twentieth century leading to local extinctions. Restrictions on harvest off California have led to at least a mild resurgence in the population (Pondella and Allen 2008; House et al. 2016) and, based on a genetics study, an effective population size of perhaps 500 individuals off southern California and northern Baja California (Chabot et al. 2015). However, there has been no direct assessment of their numbers off California.

From at least spring through fall, it is likely that most, if not all, GSB inhabit nearshore waters to depths of perhaps 30 m (Love 2011). We are interested in determining if recreational divers can assist us in determining the abundance of this species in California waters as divers can often easily approach and photograph these fish. If there was a way of identifying individuals underwater from still or video images, images from divers could help us determine the number of individuals in the sampling area. This process would require individuals to have unique markings. Giant sea bass of all ages have dark spots or blotches on their heads and flanks and these might be idiosyncratic and thus useful in identifying individuals. Among fishes, markings of various sorts, including spots and stripes, have been shown to be unique to individuals and thus may be of value in determining species abundances (Meekan et al. 2006; van Tienhoven et al. 2007; Claydon et al. 2010; Giglio et al. 2014).

To determine if we could use the spotting on the flanks of GSB as unique markers, we made preliminary observations of GSB spot patterns at the Aquarium of the Pacific in Long Beach. Here we took photographs of the three GSBs (two adults and one likely subadult) on 18 June, 1 July and 3–4 July 2014. We photographed these fish at least hourly for 12 hours (18 June, 1 July) or over 24 hours (3–4 July). Over the past few years, pattern recognition software, such as the Individual Identification System (I3S Spot 4.02; www.reijns.com/i3s, hereafter referred to as I3S), have been developed to partially automate the process of reviewing images and helping to identify individuals (van Tienhoven et al. 2007). We used I3S to compare spots on the sides of each individual and between individuals. Using both this software and visual comparisons, we found: 1) the spot patterns did not change over the 12 or 24 hours surveyed, 2) the spot patterns were unique to an individual, and 3) each pattern was unique to a side of each individual (i.e., the spot patterns were asymmetric). Soon after these analyses, we acquired from Ms. Sandy Trautwein (Aquarium of the Pacific) images taken in 2003 of two of these Aquarium of the Pacific fish. Again, using I3S and a visual inspection, we determined that the spot patterns of these individuals were identical to those observed on these

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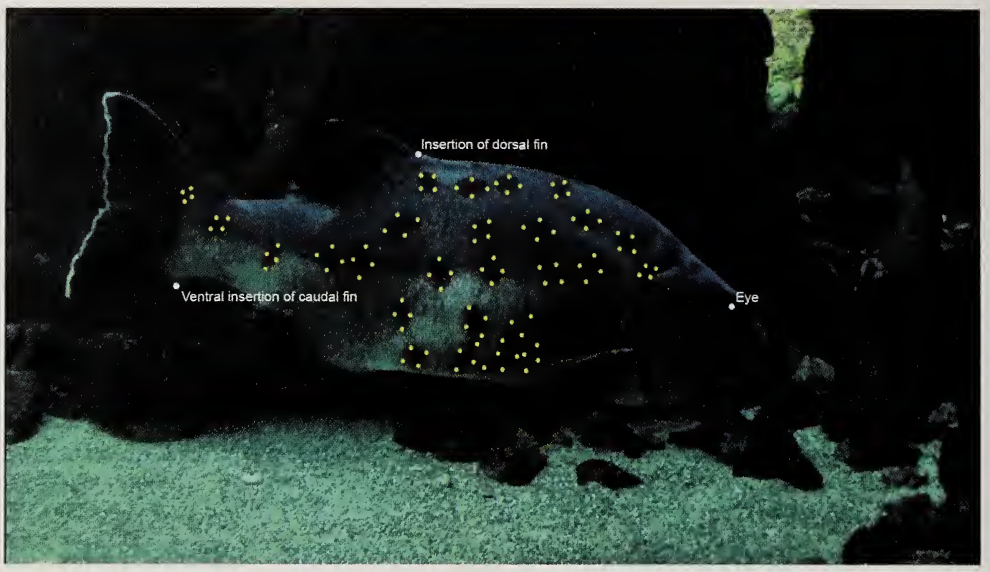

Fig. 1. An example of the spot annotations used in the I3S program. Note the position of the three reference points.

individuals in 2014. This implies that the spot patterns of adult GSB may not change over time.

Given these preliminary results we determined to answer the following questions:

1) Can I3S be used to identify individual GSB and, if so, what factors affect the ability of I3S to help identify individuals?
2) Do individual GSB have unique spot patterns?

Note that this study was limited to adult and subadult fishes. Although young red or orange fish have black spotting, they were not included in this analysis.

We created a database of known "individuals." Because each side has a unique spotting pattern in this context every fish consisted of two "individuals." For this study, we accumulated images of 35 individuals, based on 12 captive and 23 wild individuals. We validated that each wild fish was indeed unique by using scarring or other body marks. Each individual was represented by up to three unique images. When using I3S we first chose three reference points that were used for every individual. In the case of GSB, the reference points were 1) the eye, 2) the origin of the soft dorsal fin, and 3) the ventral origin of the caudal fin (Fig. 1). Then, in I3S, after marking these reference points, we annotated each spot by forming a circle around each mark (Fig. 1).

Out of 124 total tests (testing only individuals with two or more images in the reference library) we found that 93.5% of the tests ranked at least one other image of the same individual in the top 5 best matches and 94.4% of the tests ranked at least one other image of the same individual in the top 10 best matches. It is important to note that I3S does not determine a match automatically; rather the user examines the top images ranked by the software and manually determines if a match exists. In this study, I3S suggested

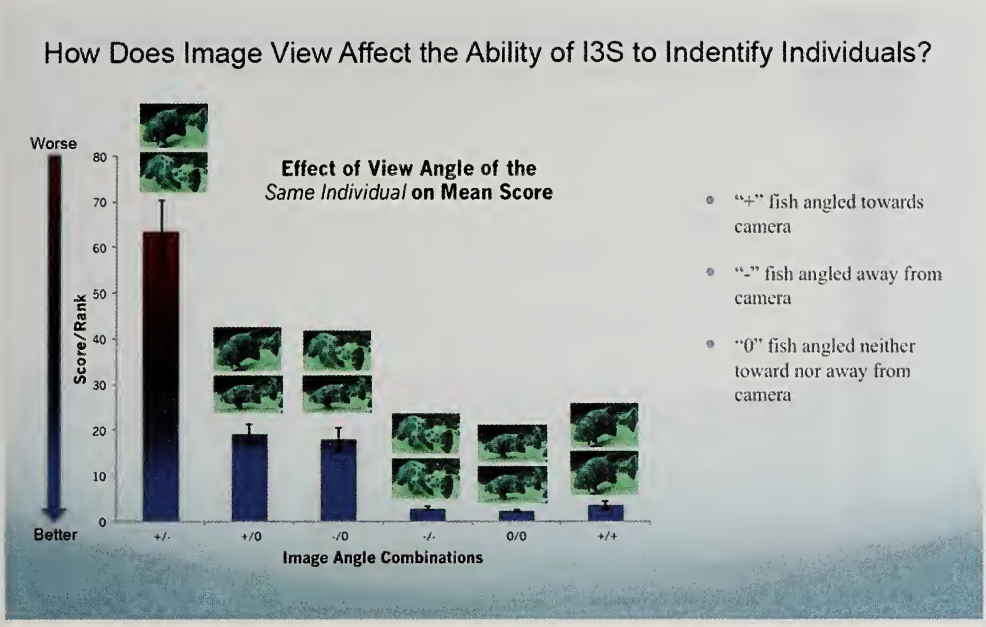

Fig. 2. The effect of comparing two images of the same fish angled differently. Higher scores imply a lower probability that the two images are of the same individual.

a correct match (placing a true match in the top 10 ranked image results) 95% of the time.

In these early tests, it was apparent that the angle at which a viewer observed an individual could affect the scores generated by, and thus the overall accuracy of, the I3S program. To test what angles were useful we sorted the scores generated by I3S for three different viewing angle combinations of the same individual. We determined that the effect of viewing angle was a large factor affecting the ability of I3S to correctly characterize two images as having come from the same individual (Fig. 2). We found that comparing images of a fish with identical orientation yielded the most accurate scores and scores increased (that is became less accurate) when the two orientations diverged. At the extreme, the highest (poorest) scores were generated when an image of a fish whose head was pointing slightly towards the camera was compared with an image of that fish with its head pointed slightly away from the camera.

We were also interested in how I3S would handle comparisons of two images where one image was of a fish perpendicular to the camera and the other was of the same fish angled to or away from the camera (Fig. 3). We found that slight divergences from the perpendicular yielded low (more accurate) scores, but that the chances of false negatives (images of two identical individuals mistaken for two separate individuals) increased as the angle increased. In particular, comparing a perpendicular image with one that was almost tail-first yielded very poor scores.

We created a database consisting of images of 16 unique individuals. Of these, 12 were captive individuals and four were photographed in the wild and identified by unique scarring. We decided to address this question by comparing the scores generated by I3S for "matching image pairs" with the scores generated for "non-matching image pairs."

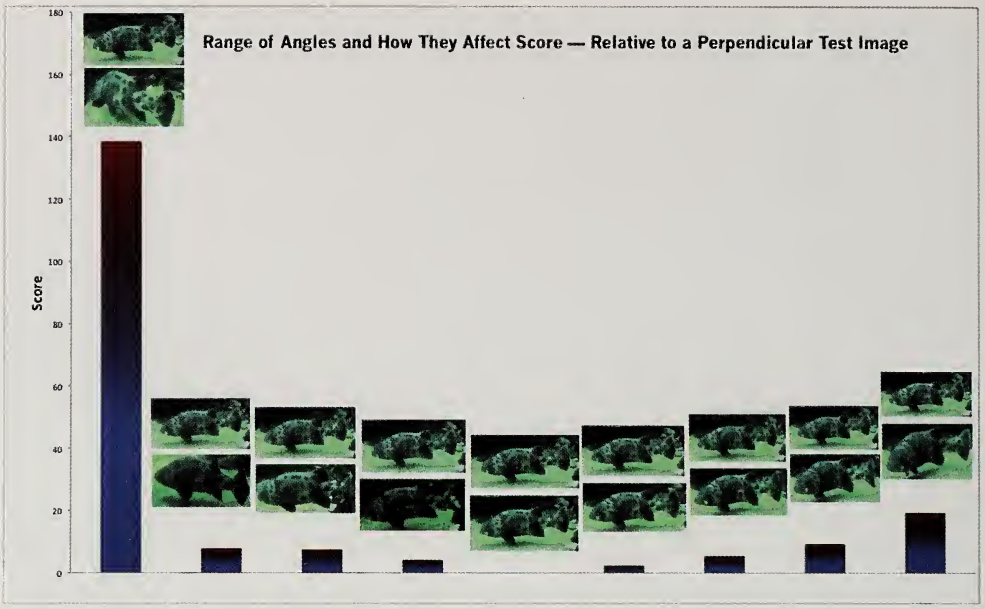

Fig. 3. Comparing the effect of two images of the same fish where one image is perpendicular to the camera and the other is variously angled away. Higher scores imply a lower probability that the two images are of the same individual.

"Matching image pairs" describes two different images of the same individual being compared with one another (72 different combinations in this study). "Non-matching image pairs" describes two different images of two different individuals being compared to one another (1568 different combinations). In this analysis we found that the populations of scores for "matching image pairs" and "non-matching image pairs" were significantly different Welch's t-test (F Ratio = 440.1338, DF = 1, Prob > F = <0.0001, t-test = 20.9795). The upper 95% confidence interval for the scores of "matching image pairs" (score = 29.3) falls well below the lower 95% confidence interval for the scores of "non-matching image pairs" (score = 105.7) (Fig. 4). Because a statistically significant difference exists between the two populations of scores generated, we can treat the spots on these fish as truly unique to the individual. In addition, the upper 95% confidence interval for the scores of "matching image pairs" also provides us with a practical cut-off score (30) for identifying matches in the program.

In summary, we have shown that using I3S can be an effective tool in helping researchers compare underwater images of unknown GSB. This software is particularly useful in winnowing through large numbers of images and providing the most likely matches. Our research implies that the spots on adult GSB are likely unique to each fish (and each side of each fish) and that these marks can aid in both creating population estimates and in understanding the species' migrations and movements. In addition, the relative ease with which recreational divers can provide us with usable images opens up this research to citizen scientists. Indeed, it is our goal to use this technique and the large number of recreational divers in southern California to census the giant sea bass population in this region.

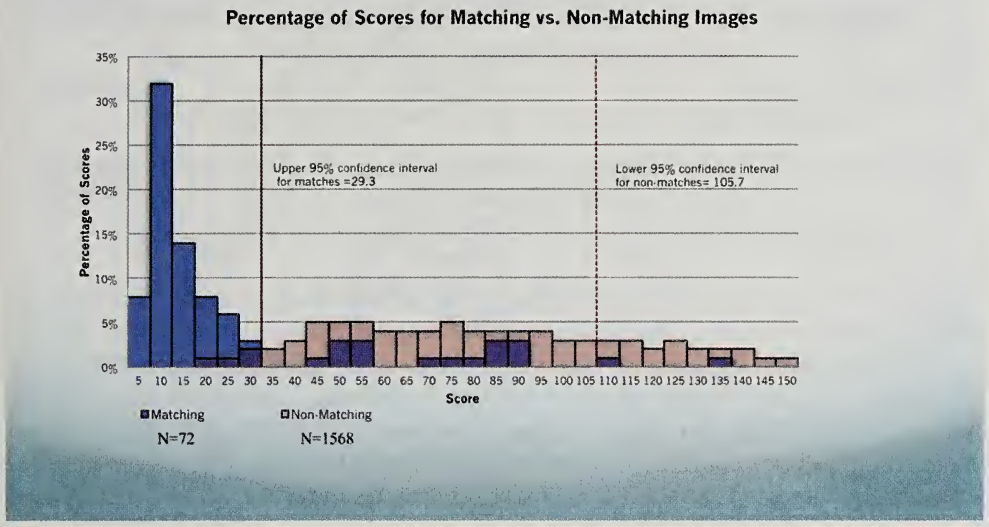

Fig. 4. The distribution of scores for "matching image pairs" and "non-matching image pairs" including their upper 95% and lower 95% confidence intervals.

Acknowledgements

We thank Sandy Trautwein for furnishing images of, and allowing us to photograph, Aquarium of the Pacific giant sea bass.

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Comparison of the Polychaetous Annelids Populations on Suspended Test Panels in Los Angeles Harbor in 1950-1951 with the Populations in 2013-2014

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Abstract.—A 14-month study was conducted of the polychaetous annelids present on attached wooden blocks at nine stations in Los Angeles Harbor in 2013-2014. The results were compared to a similar study conducted at the same stations in 1950-1951. The primary objective in both studies was to determine the location and occurrence of marine borers in the harbor. Since fouling organisms, including polychaetes, attached to the wooden blocks, it also provided an opportunity to study the polychaetes that settled on the blocks. The number of polychaete species in these two studies increased from 22 to 71. The serpulid *Hydroides elegans* was a dominate species in both studies but the pollution indicator *Capitella capitata*, common in the earlier study, was rare in the recent study. There was a seasonal occurrence in both the number of species and specimens with highs in the warmer months and lows from December through March in both studies. Many environmental changes have occurred in the Los Angeles Harbor complex over the past 63 years. New harbor piers constructed that extend into the Outer Harbor, channels have been dredged deeper and pollution abatement programs initiated. The water quality has been improved especially in the Inner Harbor as a result of these changes where the dissolved oxygen in the water was low or absent in 1950-1951 but higher (over 6.0 mg/L) in 2013-2014. This study is unusual since long-term, seasonal comparisons of marine invertebrate populations are uncommon.

Los Angeles Harbor (the Harbor) is a world port and was the site of the first study of marine pollution using benthic organisms as a measure of water quality in the United States (Anon 1952). Polychaetes were the principle benthic animals and were the subject of seasonal comparisons (Reish 1955). Published and unpublished reports of environmental studies have continued since the initial study[1,2] (Soule and Oguri 1976). The purpose of this study is to determine if there have been changes in the settlement of larval polychaetous annelids on suspended wooden test panels in Los Angeles Harbor since 1950-1951 (Reish 1971b). The earlier and present studies were done as a companion to the study of the seasonal occurrence of marine wood boring organisms (Menzies et al. 1963; Reish 1971; Reish et al. 2015). Polychaetes have served as convenient indicators of environmental water

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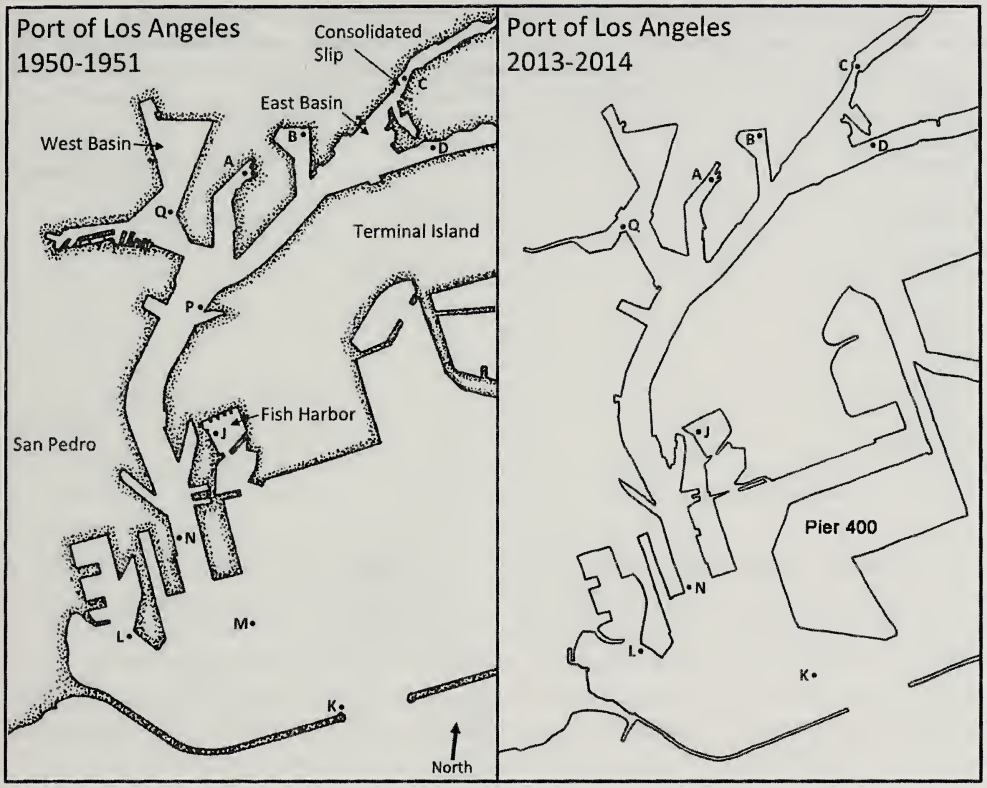

Fig. 1. Map of the Port of Los Angeles Harbor showing the station locations in the survey conducted in 1950-1951 (a). Map of the Port of Los Angeles Harbor showing the station locations for the survey of 2013-2014 (b).

conditions since the 1950s (Reish 1955). Since the earlier study was done before the initiation of pollution abatement (Reish 1971a), repeating the study will provide evidence of the effect of Harbor environmental improvement. The history of the wood-borering animals and fouling organisms in the Harbor has been detailed in Menzies et al. 1963; Reish et al. 2015. The changes in the presence of wood-borers occurred especially in the Inner Harbor and showed that pollution abatement resulted in increases of these animals where previously there were few or none (Reish et al. 2015). No study of wood-borering populations have been done between the two studies, but the wood-boring teredinids and isopod *Limnoria tripunctata* have been collected from the harbor for laboratory experiments (Eckelbarger and Reish 1973; Anderson and Reish 1967; Reish and Hetherington 1969). However, many studies have been conducted on polychaetes as fouling organisms on suspended test panels (Reish 1961; Soule and Oguri 1976), on floating docks (Crippen and Reish 1971), rock riprap[1], and soft-bottom benthos (Reish et al. 1980). Dredging of the Port of Los Angeles and Port of Long Beach complexes in the past 50 years has increased the importance of the available habitats as a nursery for nearshore fishes (Cross and Allen 1993).

Materials and Methods

The stations selected coincided in so far as possible as those selected in 1950-1951 (Reish et al. 2015 Fig. 1). The study began on 18 August 2013 and terminated on 1 October 2014.

Table 1. Dates of collection of test panels and exposure period.

Date	Short Term Period Number of Days	Long Term Period Number of Days
August 18, 2013	Initiation of Study	
September 23	28	
October 21	28	
November 18	28	
December 16	30	114
January 20, 2014	35	
March 17	56	119
May 12	28	
June 9	28	
July 14	35	
August 7	24	114
September 3	27	
October 1	28	55

Station locations described in Reish et al. (2015), noted below, and indicated in Fig. 1. One wood block (3.5 × 3.5 × 15 cm) attached to a rope, connected to a permanent harbor floating wooden structure and suspended three feet below the water surface. Wood blocks exposed, usually for 28 days, at which time removed and replaced with new blocks. A second block was attached at selected stations and exposed for a three-month period which was specifically used for the identification of teredinid wood-borers. Dominant organisms noted. Organisms scraped from the blocks, preserved in formalin and transported to the laboratory. Identification of polychaetes was by Charles Phillips and Thomas Gerlinger using procedures and taxonomic standards of the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT). Species nomenclature was based upon the SCAMIT Taxonomic Species Listing Macro and Megafauna Invertebrates for the Southern California Bight (Edition 11, 2016) and WoRMS (2017). The specific dates and length of exposure of wood blocks for both the short-and-long term periods are in Table 1. Fouling organisms scraped from the long-term exposed period for wooden blocks were nalyzed separately. Measurements made at each station each time for water temperature and dissolved oxygen concentration with CRM's YSI 556 multi-parameter meter at a depth of three feet below the water surface from the research vessel. Data were summarized by station as range and means in Reish et al. (2015).

Results

A total of 71 species/morphotypes was identified in 2013-2014 or 41 if those worms identified to family or genus are considered as immature specimens with those identified to species in comparison to those found in 1950-1951 (Table 2). There was a seasonal difference in species richness (number of species), with higher richness present from June through October 2014 and lower richness during the winter months (Table 3). The two serpulid species *Hydroides elegans* and *Neodexiospira pseudocorrugata* were found at all stations except Station K in the outer harbor but were often absent during the winter months. The nereid *Platynereis bicanaliculata* settled on the wood blocks in the Outer Harbor stations, especially Station K, from December 2013 through July 2014. *Exogone lourei, Epigamia/Myrianida* complex, and additional species of syllids, were found sporadically and at any time throughout the harbor area. The same species were also dominant on the

Table 2. Comparison of the polychaetes collected from the short term exposed blocks in 1950-1951 with those collected in 2013-2014.

Family/Species	1950-1951	2013-2014
Capitellidae		
Capitella capitata Cmplx	X	X
Chaetopteridae		
Chaetopterus variopedatus Cmplx		X
Chrysopetalidae		
Palaenotus bellis	X	
Cirratulidae		
Cirratulus sp.		X
Cirratulus spectabilis		X
Cirriformia sp.		X
Kirkegaardia siblina		X
Protocirrinereis sp.		X
Ctenodrilidae		
Ctenodrilus serratus	X	
Dorveillidae		
Dorvilleas (S.) annulata	X*	X
Ophryotrocha sp.		X
Hesionidae		
Oxydromus pugettensis	X**	
Maldanidae		
Euclymeninae	X	
Nereididae		
Neanthes acuminata Cmplx		X
Neanthes sp.		X
Nereididae		X
Platynereis bicanaliculata	X	X
Opheliidae		
Armandia brevis	X	X
Ophelina sp.		X
Polyophthalmus pictus		X
Phyllodocidae		
Phyllodoce (*Anaitides*) sp.		X
Eteone sp.	X	
Eulalia quadrioculata		X
Eumida sanguinea	X	
Phyllodoce sp.		
Phyllodocidae		X
Phyllodoce longipes		X
Phyllodoce medipapillata		X
Polynoidae		
Halosydna johnsoni		X
Halosydna brevisetosa	X	X
Harmothoe imbricata Cmplx		X
Lepidonotus sp.		X
Lepidontinae		X
Polynoinae		X
Sabellidae		
Bispira sp.		X
Euchone limnicola		X
Fabricidae		X
Paradialychone ecaudata		X
Parasabella sp.		X
Parasabella fullo		X
Pseudopotamilla sp.		X
Sabellinae		X

Table 2. Continued.

Family/Species	1950-1951	2013-2014
Serpulidae		
Hydroides sp.		X
Hydroides elegans	X***	X
Hydroides gracilis		X
Neodexiospira eximia		X
Neodexiospira pseudocorrugata		X
Protolaeospira eximia		X
Serpulidae		X
Spirorbinae		X
Spionidae		
Boccardia proboscidea	X	
Carazziella sp.	X	
Dipolydora socialis		X
Polydora sp.		X
Polydora cornuta		X
Polydora limicola	X	X
Prionospio sp.		X
Prionospio heterobranchia		X
Prionospio pygmaeus		X
Pseudopolydora paucibranchiata		X
Pseudopolydora sp.		X
Spionidae		X
Syllidae		
Brania brevipharyngea		X
Epigamia/Myrianida Cmplx		X
Eusyllis sp.		X
Eusyllis transecta	X	
Eusyllinae		X
Exogone dwisula		
Exogone lourei	X	X
Exogone sp.		X
Megasyllis nipponica		X
Odontosyllis phosphorea	X	
Proceraea prismatica	X	
Salvatoria californiensis		X
Sphaerosyllis californiensis		X
Syllis gracilis Cmplx	X	X
Typosyllis sp.		X
Typosyllis alternata		X
Typosyllis heterochaeta	X	
Typosyllis fasciata	X	
Typosyllis variegata		X
Terebellidae		
Eupolymnia heterobranchia		X
Pista brevibranchiata		X
Polycirrus sp.		X
Nicolea sp.	X	
Terebellinae		X
Total number of species/morphotypes	22	71_

*Reported as *Stauronereis rudolphi*.
**Reported as *Ophiodromus pugettensis*.
***Reported as *Hydroides pacifica*.

Table 3. Seasonal occurrence of the number of species by station collected on the short-term exposure periods in 2013-2014 collection dates.

	9/13	10/13	11/13	12/13	1/14	3/14	4/14	5/14	6/14	7/14	8/14	9/14	10/14
A	19	12	2	0	1	1	3	1	23	39	53	33	49
B	15	17	15	9	10	6	10	1	41	35	29	28	19
C	11	21	13	4	2	7	7	1	13	13	12	10	13
D	20	31	6	2	0	5	5	1	55	26	15	7	17
J	28	31	12	7	4	8	47	2	138	37	14	30	46
K	0	5	2	5	8	2	5	0	9	8	0	0	4
L	0	7	1	8	5	10	17	2	21	18	7	5	7
N	5	4	6	1	2	8	9	1	3	27	3	4	3
Q	0	7	3	1	1	0	1	1	1	12	3	4	11

long-term exposed wood blocks with the addition of the sabellid *Paradialychone ecaudata.* Data are summarized by station with the dominant polychaetes species indicated.

Station A in Inner Harbor Slip 1: 240 specimens, 19 species (Table 2). Peaks in numbers occurred in Fall 2013 and Spring-to-Fall in 2014. The serpulids *Hydroides* and *Neodexiospira* species dominated with occasional occurrences of different species of syllids. Station B in Inner Harbor Basin 5: 243 specimens, 22 species. *Hydroides* and *Neodexiospira* dominated during the wormer months. Station C in Consolidated Slip: 122 specimens, 25 species. The serpulids *Hydroides* and *Neodexiospira* and the syllid *Exogone lourei* were the principle species. *Exogone* dominated the December-January period with the two serpulids dominating the rest of the year. Long-term test panels were exposed for three time periods extending from January through October 2014. There was a diversity of species of which 31 species and 223 specimens were present with the serpulid *Neodexiospira pseudocorrugata,* the syllids *Exogone lourei* and *Epigamia/Myrianida* complex dominating the abundances. Station D in Cerritos Channel: 196 specimens, 18 species. No species were dominant. However, many *Hydroides elegans* were present in the November and June collection periods but absent from the other periods. The syllids *Exogone lourei* and the species complex of *Epigamia/Myrianida* were present occasionally in small numbers. A total of 32 species and 320 individuals were taken from the four test panels exposed for the longer period of time. Serpulid species were the most common followed by different syllid species. Members of nereids, polynoids, sabellids, and spionids were also present. Greater numbers were present in the fall and spring months. Station J in Fish Harbor: 142 specimens, 29 species. *Hydroides elegans* accounted for 87% of the polychaetes collected. Peak abundances of this species were in fall 2013 and June through October 2014. Station K in the Outer Harbor at a channel marker: 50 specimens, 12 species. The nereid *Platynereis bicanaliculata* was the most common species taken which was present in all collection periods except the fall 2013. *Platynereis* accounted for 50% of the specimens taken from the short-term test panels and 26% from those exposed for the longer periods. A total of 136 specimens in 19 species was collected from the long-term exposed panels. Station L at the entrance to West Basin near the Fire Station: 114 specimens, 23 species. *Platynereis bicanaliculata* and the syllid *Exogone lourei* accounted for 50% of the specimens present on the short-term test panels. A total of 34 species and 294 specimens were taken from the four long-term test panels which was dominated by *Hydroides elegans, Paradialychone ecaudata, Exogone lourei* and *Platynereis bicanaliculata.* Station N at the Port Pilot station in the Main Channel: 76 specimens, 16 species. Three species accounted for 70% of the specimens collected from the

Table 4. The number of species and specimens collected from the longterm test panel exposure period in 2013-2014 by station and date (as months).

	9-12 (2013)	12 (2013) - 4 (2014)	4-8 (2014)	8-10 (2014)
C	*	18-78	13-82	19-63
D	9-140	13-66	20-101	4-13
K	17-90	8-22	6-14	6-10
L	26-132	13-40	10-76	13-46
N	26-264	9-36	11-60	5-11
Totals	33-626	31-252	39-233	26-143

*No data.

short-term test panels: *Hydroides elegans, Neodexiospira pseudocorrugata,* and *Platynereis bicanaliculata.* A total of 30 species and 371 polychaetes was collected from the long-term test panels that were numerically dominated by *Paradialychone ecaudata.* Station Q near the entrance of West Basin: 55 specimens, 12 species. Serpulids and spirorbids accounted for over 50% collected from the test panels.

The water temperature at the nine stations ranged from a low of 11.3°C at Station L in April 2015 to a high of 22.6°C at Station J in September 2014 with a nine stations medium of 17.6°C. The dissolved oxygen levels ranged from a low of 6.0 mg/l at Station D in August 2013 to a high of 10.6 mg/l at Station A in December 2013 with a nine stations medium of 7.6 mg/l (Reish et al. 2015).

Discussion

Comparison of the polychaete populations in 1950-1951 to 2013-2014 indicated a difference in species richness: 22 species compared to 71 species/morphotypes in the later study (Table 2; Fig. 2). *Polydora limicola, Capitella capitata* and *Hydroides pacificus* [= *H. elegans*] were the three most common species in 1950-1951 with peak abundances occurring in the spring months. A suppression in the number of species occurred whenever the dissolved oxygen concentration fell below 4.0 mg/L. Seven common occurring species were present whenever the dissolved oxygen was above this concentration. It is significant that three test blocks were suspended at three different levels at a station in the earlier study compared to only one level in the present study. *Hydroides elegans* was the only common species to both studies. *Neodexiospira pseudocorrugata* and the other small spirorbid species noted in 2013-2014 were not present in the earlier study. Presumably, they were not predent from the test panels or, if present, were smashed in the process of scraping. Only 18 *Capitella capitata* [= *C. capitata* complex], a common pollution indicator species, were present on the test panels exposed in 2013-2014 compared to 141 in the earlier study. Seasonal differences were similar in both studies with peaks in species numbers in the warmer months and lowest during the winter season as indicated in Fig. 2. The seasonal settlement of *Platynereis bicanaliculata* was the same in both studies. Only a few syllids occurred in 1950-1951.

The greater diversity of polychaetes now compared to 1950-1951 reflects the improvement of water and sediment quality that has occurred because of ship channel deepening, the removal of contaminated sediments and sources of pollution, and an improvement of water circulation (Soule and Oguri 1976). A suppression in the number of polychaete species was noted whenever the dissolved oxygen concentration was less than 4.0 mg/L in 1950-1951; it was always above 6.0 mg/L at all stations in 2013-2014 which is above

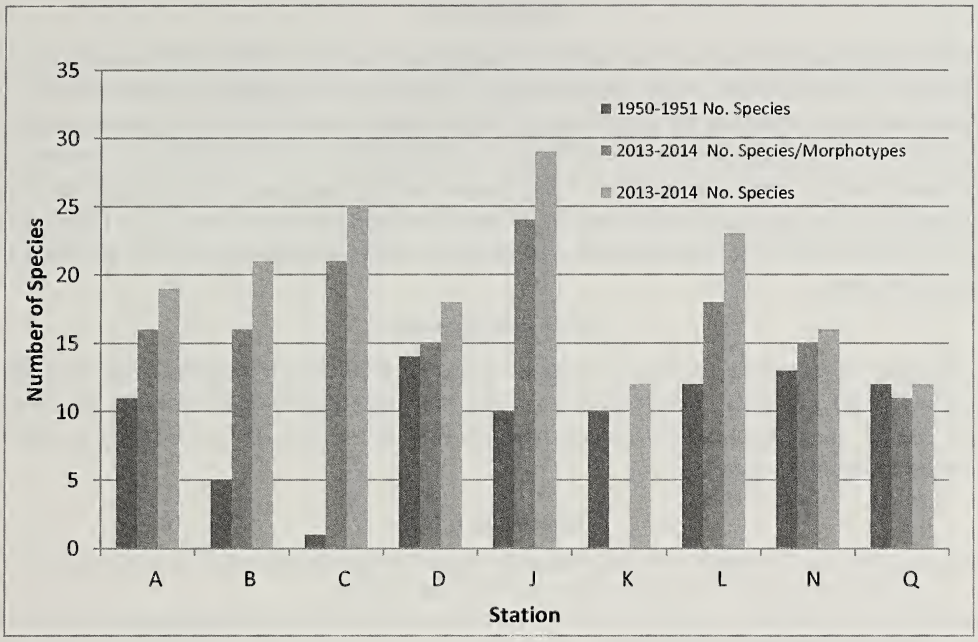

Fig. 2. Comparison of the Number of Species/Morphotypes by Station Collected from Short-Term Exposure Periods on wood blocks in 2013-2014 Compared with 1950-1951.

the level considered necessary for fish life. The polychaete *H. elegans* was the most abundant species in 2013-2014, but it did not compare to 1956 when the pictures were taken of the settlement of this species on a gallon jar after a 28-day exposure period in the harbor (Reish 1961, plate 2, Figs. 2 and 4). These findings agree with the environmental study conducted by MEC Analytical Systems, Inc. (2002) of Los Angeles-Long Beach Harbors. They noted that there has been a steady improvement in the habitat quality as demonstrated by improvement of species diversity and less dominance by pollution tolerant benthic species in the past half century. Rock riprap communities have been relatively stable in the in the past half century. Kelp was restricted primarily to the Outer Harbor breakwater and its coverage has increased since 1986 (MEC 2002). Harbor dredging in the past century has increased the habitat and nursery area for inshore marine fishes (Cross and Allen 1993).

The number of species was greater at all nine stations except Station Q, which remained unchanged but lacked the pollution tolerant species *Capitella capitata.* The largest difference was noted at Stations A, B and C. This was the result of the elimination of waste discharges originating from Dominguez Channel and discharged into Consolidated Slip above Station C. *Capitella capitata* was the only species present in 1950-1951 whereas 25 species were present in the recent study. The number of species increased from 10 to 24 at Station J because of the cessation of cannery waste discharges in Fish Harbor (Reish et al. 1983). An increase in the number of species present in 2013-2014 was expected since environmental improvement in Consolidated Slip was first reported in Reish (1971a) one year after all discharges were eliminated. Thirteen invertebrate species were collected from the floating docks at Station C of which three were polychaetes. *Hydroides* was the dominant species; *Capitella capitata* was not present.

Conclusions

The numerical increase in the number of polychaete species in 2013-2014 compared to 1950-1951 was the result of the improvement in harbor water quality. The elimination of waste discharges entering the Consolidated Slip increased the dissolved oxygen concentration from zero, or near zero in 1951-1952 to over 6.0 mg/l in 2013-1014. The improvement of water quality enabled a diversity of polychaete larvae to migrate into the Inner Harbor and settle on the test panels. The number of species present increased from 22 in 1950-1951 to 71 in 2013-2014. The serpulid *Hydroides elegans* was the dominant species in the Harbor in both studies.

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Cover: Short-finned pilot whales observed off Palos Verdes, California, in December 1986, showing distinctive features used in photo-identification. Photo by A. Schulman-Janiger.